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SEASONAL VARIATIONS IN ABUNDANCE OF CERTAIN ESTUARINE AND MARINE FISHES IN LOUISIANA, WITH PARTICULAR REFERENCE TO LIFE HISTORIES

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CONTENTS

SEASONAL VARIATIONS IN ABUNDANCE OF CERTAIN ESTUARINE AND MARINE FISHES IN LOUISIANA, WITH PARTICULAR REFERENCE TO LIFE HISTORIES[1]

INTRODUCTION

At the inception of the Shrimp Investigations of the United States Bureau of Fisheries, which were begun in Louisiana in 1931, in cooperation with the Louisiana Department of Conservation, it was apparent that data on other animals of this area could be collected along with those on shrimps. Such material is of value for its own sake and as a supplement to the primary investigation. This paper treats of some of the data on fishes collected in trawls from October, 1931, to March, 1934, covering a period of two and a half years.

The writer wishes to acknowledge his indebtedness to all people connected with the Shrimp Investigations in Louisiana, many of whom have assisted in innumerable ways.

Aims

The objects of this work were:

1. To study the destruction of fish by trawls with the view of learning something of the number, species and relative importance of fishes destroyed in Louisiana by shrimp fishermen, who take about ninety per cent of their catch in trawls. This problem has been considered by Gunter (1936).

2. To study the natural history of such fishes as would be taken in the trawls by:

a—Analyses based on abundance, with which the present paper is chiefly concerned. b—The study of relative numbers of the various species (Gunter, 1938). c—Studies of the environment, as evidenced by hydrographic data.

COLLECTION OF DATA

The objects of the work can be more clearly understood if some of the characteristics of the area studied are known. The following is a brief account.

The territory selected for intensive study was Barataria Bay and the adjacent waters of the Gulf of Mexico. The choice of this area was determined by its accessibility and the extensive shrimp industry located there. Barataria Bay is shallow (2-12 feet deep), soft-bottomed, has several islets, and is located in the heart of the Louisiana coastal marsh about forty miles northwest of the mouth of the Mississippi River. It is connected with the Gulf of

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Mexico by a number of narrow passes. The depth of gulf waters increases very gradually, so that twelve miles from shore it is only ten to twelve fathoms.

The method of collecting data has been stated by Weymouth, Lindner and Anderson (1933), and only the essentials will be given here. Five stations were selected and visited on an average of twice each month. These ranged from the brackish headwaters of Barataria Bay to six miles out in the open gulf. The map (Fig. 1) shows the stations marked in heavy lines. The

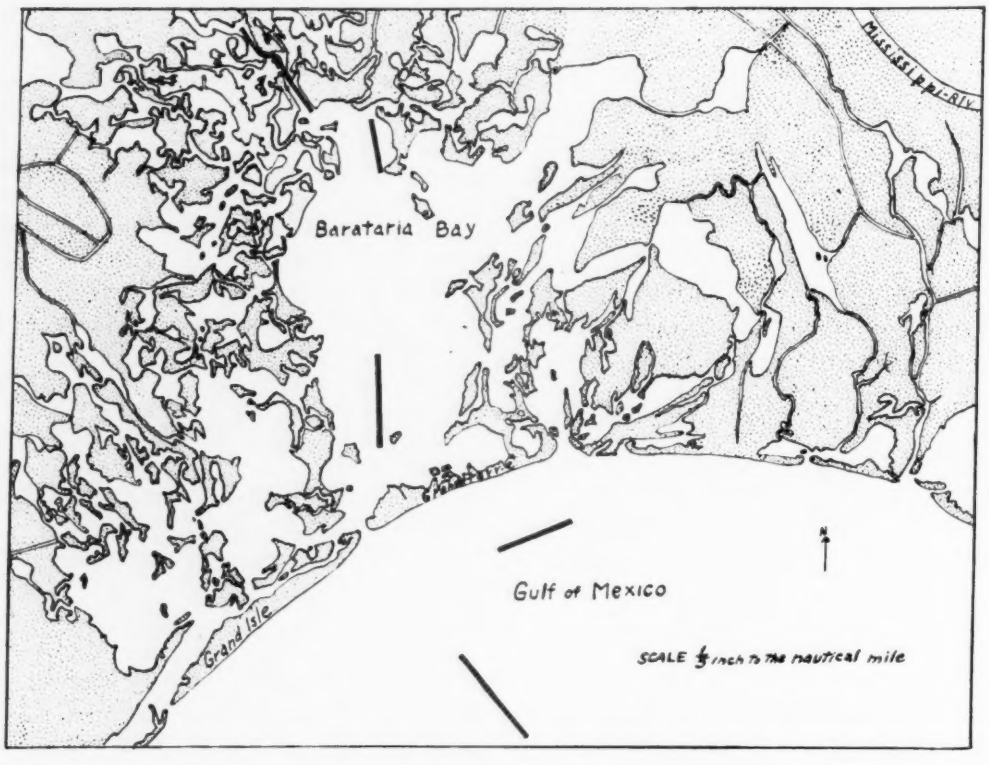

FIGURE 1.
Map of Barataria Bay and adjacent waters. The stations are marked in heavy lines.

first covers the lower end of Bayou St. Denis. The next one extends from Myrtle Grove Canal to St. Mary's Point. The following station is from Middlebank Light to Independence Island. The first station in the Gulf of Mexico paralleled the beach one mile offshore and extended from Quatre Bayou Pass to another pass called Coup à Belle. The second outside station was from three to six miles southeast of Barataria Pass. Whenever it was deemed worthwhile other hauls were made in various places, but not with the regularity that the five main stations were visited. Data from the places visited irregularly are not given here.

At each place a drag was made with an ordinary otter trawl of thirty-five feet wingspread and a mesh measuring three quarters of an inch square. The

hauls were approximately of one hour's duration. A hydrographic station was made at each drag by Louisiana Department of Conservation officials. The material caught was placed on the aftdeck of the boat and separated into piles according to species. Counts of each species were made and recorded. Notes on the size were made. The present data are almost wholly on abundance as derived from actual counts in trawl hauls.

Occasionally, the trawls would become so full of shrimp or jellyfish in the full period drag that they could not be raised, so it became necessary to cut the length of haul to one-half or one-fourth of the usual time. At other times sharks and porpoises tried viciously to get at fish within the trawl and in so doing cut large holes in the bag. The trawl was sometimes left down only a short while to avoid the actions of these predators. Whenever the time was cut short the numbers of fish were weighted, so that they were made as nearly equivalent to a full time haul as possible. Rarely there were a great many fishes and a limited time to count them, so they were divided into two equal piles and one-half of them counted. This number was then multiplied by two to make it equivalent to a whole haul. Obviously, this is not strictly accurate, but the writer believes that the percentage of error in a large number of fishes is negligible for purposes of this paper.

The advantages of this method of collecting data are: (1) The regular collection of samples was at set stations covering a wide range of conditions from almost fresh to pure sea water, over a period of time which shows seasonal fluctuations at a given station. (2) The otter trawl is especially fit for the catching of slow-moving bottom forms. It is less efficient for catching fast-swimming active fishes, although the young animals of this type are sometimes taken in abundance. Specimens caught ranged in size from post-larval anchovies to a 300-pound spotted whip-ray. Taken all around the otter trawl seems to be as useful in this type of study as any single unit of gear that could be devised. Although it is inefficient in clear water as pointed out by Beebe (1934), the coastal Louisiana waters are generally of high turbidity.

EXPOSITION OF DATA

Tables giving the actual count of specimens taken would fill a large volume. There is not room for them here so another method of presentation is used. All hauls for a given month were thrown together and the total number of every species was divided by the number of hauls. This gave the average number of each species taken per drag for each month. The numbers are given in Tables 1 and 2. The curves were made from these tables. The numbers of hauls are given for every month for both the bay and the gulf in Table 3.

Unfortunately, in some months hauls were not made. Those missing are November and December, 1931; and January, 1932, for the gulf; and March, 1934, for the bay. In February, 1932, no hauls were made.

TABLE 1. AVERAGE NUMBER OF FISHES TAKEN PER HAUL, BY MONTHS, IN BARATARIA BAY

	1931			1932												1933												1934	
	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Achirus lineatus	2.0	....	6.0	....	....	....	....	0.5	0.3	....	....	8.0	12.8	2.5	0.2	0.1	0.7	0.2	0.2	1.1	....	0.1	....	0.2	6.4	2.6	0.3	....	0.3
Anchoviella epsetus	1.0	11.3	27.7	10.7	....	77.7	92.6	39.1	15.3	13.0	34.7	2.2	23.7	8.7	76.7	68.1	76.4	30.2	47.7	13.6	1.8	19.5	18.3	3.7	17.4	5.9	19.5	28.6	2.0
Bagre marinus	1.5	....	....	....	....	....	0.3	0.4	3.1	2.2	13.1	66.5	4.5	0.5	....	0.1	0.1	0.2	0.2	1.0	1.0	1.6	9.6	36.2	11.8	....	....	....	71.3
Bairdiella chrysura	4.5	4.0	12.0	74.8	....	1.0	0.4	....	0.6	1.0	11.3	0.2	3.9	2.0	0.9	0.4	2.1	0.2	0.3	1.3	0.2	31.8	5.0	0.8	1.8	13.1	3.3	21.1	....
Brevoortia patronus	6.0	5.7	15.3	220.5	....	30.8	30.2	3.9	0.9	0.2	1.4	12.5	4.5	13.8	39.7	39.7	11.3	7.5	11.9	7.7	1.8	5.2	61.3	5.0	31.8	11.1	34.3	102.8	191.0
Caranx hippos	....	....	....	....	....	....	....	....	....	0.2	2.6	0.2	....	....	....	....	....	....	....	....	....	....	1.6	0.2	0.1	0.1	....	....	....
Chloroscombrus chrysurus	0.5	....	....	....	....	....	....	....	....	....	1.7	0.2	0.5	....	....	....	....	....	....	....	....	....	0.3	....	3.9	....	....	....	....
Citharichthys spilopterus	....	2.0	3.3	....	....	0.1	....	0.7	3.2	1.3	8.7	42.5	3.7	1.8	0.6	....	....	0.5	0.2	2.8	....	....	0.4	....	33.9	4.9	1.3	....	1.3
Cynoscion arenarius	4.5	11.0	2.0	8.0	....	1.3	1.3	17.5	57.6	13.7	114.9	21.2	50.6	7.2	4.1	0.3	1.1	1.8	4.5	43.7	24.0	44.5	39.3	42.3	15.7	15.6	12.0	1.8	6.7
Cynoscion nebulosus	....	....	4.0	10.2	....	3.4	0.6	0.3	0.3	0.7	0.1	1.0	1.8	7.7	7.7	33.7	12.7	1.5	1.1	1.3	0.5	0.1	0.3	0.2	0.9	1.6	1.0	6.8	8.7
Cynoscion nothus	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1.7	0.1	....	....	....	2.9	....	....	....	....	....	....	....	....	....
Dasyatis sabina	....	....	....	0.7	....	....	....	....	0.2	....	0.1	0.7	0.2	0.7	....	0.1	1.5	....	0.1	....	1.0	0.4	0.1	0.2	0.4	0.1	0.2	....	....
Etropus crossotus	....	2.0	4.0	2.5	....	3.6	....	0.2	0.9	0.2	3.4	86.0	5.6	7.2	....	....	2.9	1.2	0.2	0.7	....	1.9	0.9	1.0	10.0	2.0	0.2	....	....
Galeichthys felis	1.5	18.0	35.7	0.5	....	7.3	5.0	11.1	18.7	7.0	28.3	66.8	34.8	35.3	8.8	0.3	18.3	17.9	14.1	21.0	10.7	8.5	8.9	12.8	34.1	5.6	4.2	1.5	13.3
Larimus fasciatus	....	....	....	....	....	....	....	0.1	....	....	....	....	0.1	0.3	0.1	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Leiostomus xanthurus	1.5	0.3	0.7	4.5	....	1.4	....	6.4	15.1	7.3	7.7	2.3	4.8	0.7	0.1	....	0.1	0.2	1.1	25.8	4.0	12.2	89.9	7.2	9.0	12.1	1.7	42.3	22.7
Menticirrhus americanus	....	....	0.3	....	....	0.3	0.3	0.5	0.3	0.3	0.4	3.3	4.0	1.2	0.1	....	0.6	0.2	....	3.3	0.8	0.5	....	0.7	1.0	1.6	....	0.2	0.3
Micropogon undulatus	4.5	0.3	5.7	27.7	....	46.3	34.1	197.5	344.8	163.2	136.6	125.0	5.5	0.8	12.2	14.9	77.8	241.6	495.0	813.7	20.2	217.2	159.1	63.3	26.6	3.7	0.3	5.5	79.7
Paralichthys lethostigmus	....	....	0.7	3.0	....	1.6	1.1	1.4	2.1	0.7	1.0	1.3	0.8	0.3	0.2	....	....	0.3	0.6	2.3	2.8	1.5	2.6	0.8	1.7	0.3	....	0.3	0.3
Polynemus octonemus	....	....	....	....	....	....	....	2.6	6.7	4.0	15.3	14.7	1.8	....	....	....	....	....	....	11.1	59.9	1.3	72.1	29.6	7.3	1.7	....	....	....
Poronotus triacanthus	....	....	....	....	....	1.0	0.9	0.2	....	0.2	....	0.3	1.1	....	0.2	....	0.2	13.0	8.4	15.1	8.2	1.2	1.3	....	....	....	....	0.2	1.0
Selene vomer	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Signalosa atchafalayae	....	....	0.7	3.5	....	0.6	0.6	0.1	0.2	0.3	0.1	3.7	2.5	0.5	10.3	2.0	2.8	0.5	....	0.1	....	1.5	2.0	1.2	3.0	1.0	....	3.2	5.0
Stellifer lanceolatus	....	....	5.3	....	....	....	....	....	3.3	....	0.3	97.8	5.9	0.8	....	0.4	0.1	....	0.4	1.3	0.7	51.1	0.6	6.0	42.3	0.4	....	....	....
Symphurus plagiusa	....	0.3	1.0	0.3	....	....	0.1	0.1	....	....	1.3	25.2	2.1	1.0	0.1	0.4	0.1	....	0.4	1.3	0.7	0.1	....	0.7	3.3	0.6	....	0.7	....
Trichiurus lepturus	2.0	0.7	0.7	0.3	....	0.2	2.6	1.1	4.0	1.2	0.7	2.8	3.5	0.2	0.1	0.3	0.2	1.5	0.5	12.2	1.8	29.4	34.9	35.0	9.6	5.9	3.0	6.3	2.0
Trinectes maculatus	0.5	1.3	20.7	0.3	....	2.0	0.7	2.0	1.9	0.5	4.3	28.7	8.6	3.8	0.3	2.6	4.7	19.5	19.8	35.0	0.2	6.4	5.3	1.5	13.4	3.0	0.7	0.7	1.7
Urophycis floridanus	....	....	....	....	....	0.1	0.5	....	....	....	....	....	....	....	0.4	1.4	3.2	1.6	0.6	0.3	....	....	....	....	....	....	....	....	....	....
Vomer setapinnis	41.5	0.7	0.3	....	....	....	....	....	0.1	2.8	9.1	18.0	6.1	0.2	....	....	....	....	0.1	....	....	0.9	8.0	26.3	65.6	....	....	....	....

TABLE 2. AVERAGE NUMBER OF FISHES TAKEN PER HAUL, BY MONTHS, IN THE GULF OF MEXICO

	1931	1932											1933												193		
	O	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
Achirus lineatus	....	0.7	0.6	1.3	2.3	0.2	.....	.....	1.5	2.3	....	....	0.8	0.7	0.1	....	.....	.....	.....	.....	0.3	0.3	1.0	.....	2.0	....
Anchoviella epsetus	0.8	39.0	63.0	10.41	39.2	8.5	15.0	8.3	2.4	5.0	20.0	17.4	32.1	7.2	16.8	....	0.3	36.5	33.1	12.7	15.7	18.7	29.0	48.8	13.5	1.0
Bagre marinus	....	....	....	.....	0.5	.....	.....	.....	4.5	1.8	4.3	0.3	0.8	1.8	0.9	....	.....	11.5	21.5	31.3	0.7	2.3	1.0	.....	.....	....
Bairdiella chrysura	....	9.0	0.1	2.9	4.5	1.2	1.3	.....	0.5	3.3	3.0	2.4	3.8	0.1	5.5	....	11.0	4.0	0.5	.....	.....	0.7	3.3	0.2	....	1.0
Breevoortia patronus	0.5	0.7	6.1	0.9	2.8	6.0	1.3	.....	0.8	1.8	1.3	0.7	0.8	1.3	4.0	1.0	4.7	58.0	2.1	3.3	2.7	1.3	3.3	8.0	.....	....
Caranx hippos	0.3	....	....	.....	.....	1.2	.....	1.3	....	1.0	....	.....	.....	.....	0.5	.....	.....	.....	.....	.....	.....	0.3	.....	.....	.....	.....
Chloroscombrus chrysurus	....	....	....	.....	.....	.....	.....	2.5	2.9	2.3	0.3	.....	.....	34.7	.....	.....	.....	.....	0.9	.....	4.0	8.7	0.7	.....	.....	.....
Citharichthys spilopterus	....	....	....	.....	0.5	.....	.....	2.0	1.8	0.3	....	.....	.....	2.0	.....	.....	.....	.....	0.1	.....	5.3	....	1.3	0.2	1.5	22.0
Cynoscion arenarius	10.8	....	3.4	5.7	80.8	71.8	13.7	35.8	28.3	18.8	44.7	1.4	38.6	7.2	25.6	4.0	21.3	.....	58.9	36.7	28.0	29.0	79.7	3.2	9.5	3.0
Cynoscion nebulosus	....	3.7	....	.....	.....	.....	.....	.....	.....	.....	.....	0.7	0.3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	....
Cynoscion nothus	....	.....	0.1	.....	1.3	.....	111.3	.....	5.3	1.5	11.7	4.0	11.9	9.8	5.3	1.0	.....	43.0	18.4	1.0	.....	.....	.....	.....	0.4	....
Dasyatis sabina	....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.9	.....	.....	.....	.....	0.3	.....	.....	.....	.....	.....	.....	.....	0.5	....
Etropus crossotus	....	3.3	0.1	0.1	0.2	1.0	.....	9.8	1.9	1.5	1.0	9.3	4.0	1.0	.....	1.0	.....	21.5	3.1	0.7	0.3	0.7	3.3	1.8	6.0	....
Galeichthys felis	0.8	0.3	4.8	3.3	9.3	7.8	10.7	40.0	12.4	7.0	26.0	29.0	13.3	22.2	6.1	....	65.7	12.0	10.1	8.7	4.3	9.0	9.7	5.2	7.0	....
Larimus fasciatus	0.3	.....	.....	0.2	3.2	2.0	9.7	2.3	3.8	0.8	0.3	0.6	0.6	.....	.....	.....	.....	0.5	5.9	.....	0.3	1.3	.....	1.0	2.0	....
Leiostomus xanthurus	0.5	.....	.....	2.6	48.3	75.0	1.7	3.0	0.6	1.3	0.3	1.3	.....	.....	37.9	.....	12.3	10.5	11.9	2.0	0.7	3.3	3.7	116.0	5.5	....
Menticirrhus americanus	0.5	.....	2.6	0.3	2.7	1.7	.....	9.0	11.6	3.3	17.0	....	44.6	34.2	3.9	....	6.3	8.5	1.2	3.3	0.7	21.0	6.7	5.0	7.0	3.0
Micropogon undulatus	17.5	115.3	3.5	271.6	446.0	451.5	472.0	1728.0	683.1	129.3	55.0	5.0	0.3	1.0	65.1	35.0	696.0	353.5	291.2	47.7	22.3	43.7	329.3	2.4	1.0	70.0
Paralichthys lethostigmus	....	1.7	....	.....	0.2	.....	.....	.....	.....	.....	.....	0.1	.....	.....	.....	1.0	2.3	0.5	.....	.....	.....	.....	.....	.....	1.0	1.0
Polynemus octonemus	5.0	....	....	3.7	23.0	21.7	2.7	14.3	7.6	.....	....	.....	.....	.....	0.8	2.0	9.3	24.0	26.7	1.7	1.0	....	.....	.....	.....	....
Poronotus triacanthus	0.3	.....	2.1	0.1	0.2	.....	.....	.....	.....	0.3	3.7	1.0	20.5	49.7	28.5	10.0	26.3	7.0	0.1	.....	.....	.....	.....	0.4	0.5	....
Selene vomer	33.8	1.0	1.1	.....	.....	.....	.....	11.5	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	....
Signalosa atchafalayae	....	1.0	0.4	.....	.....	.....	.....	.....	.....	0.8	1.7	0.6	0.1	0.8	.....	.....	1.3	.....	0.1	.....	0.3	0.7	.....	5.4	4.5	....
Stellifer lanceolatus	9.3	.....	1.8	18.2	107.5	106.7	61.7	315.5	135.5	57.3	42.3	18.3	22.9	19.7	28.5	35.0	39.3	222.0	171.0	101.3	50.3	31.3	40.3	2.6	59.5	1.0
Symphurus plagiusa	0.3	.....	0.1	0.5	0.5	.....	.....	13.8	1.4	0.5	....	4.6	2.6	1.0	0.5	2.0	.....	.....	0.4	.....	.....	.....	2.3	.....	1.0	14.0
Trichiurus lepturus	8.0	9.3	2.4	35.1	56.3	55.7	24.3	30.8	5.8	9.8	39.7	12.7	33.1	17.2	18.9	3.0	2.7	44.0	56.0	28.0	5.0	7.3	25.0	4.6	50.5	6.0
Trinectes maculatus	0.3	1.0	5.0	3.5	6.5	5.5	7.3	52.0	14.9	0.5	3.3	7.3	13.1	28.0	2.4	2.0	1.3	0.5	1.0	0.3	0.7	5.3	6.3	0.6	2.0	1.0
Urophycis floridanus	....	....	0.1	.....	.....	.....	.....	.....	.....	.....	.....	1.3	2.9	1.5	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1.0	1.0
Vomer setapinnis	19.3	0.7	....	0.9	0.2	12.3	4.7	1.5	11.3	3.8	15.3	1.9	1.8	60.7	19.1	....	.....	1.0	45.6	38.3	126.0	11.0	3.0	0.8	5.5	5.0

TABLE 3. NUMBER OF HAULS MADE EACH MONTH AT STATIONS IN BARATARIA BAY AND THE GULF OF MEXICO

Months	1931		1932		1933		1934	
	Bay	Gulf	Bay	Gulf	Bay	Gulf	Bay	Gulf
January	..	..	5	0	7	7	6	5
February	..	..	0	0	12	8	3	2
March	..	..	9	3	12	8	0	1
April	..	..	12	8	11	8	..	..
May	..	..	14	10	9	1	..	..
June	..	..	9	6	6	3	..	..
July	..	..	6	8	10	4	..	..
August	..	..	7	3	7	8	..	..
September	..	..	7	6	6	3	..	..
October	2	4	12	8	7	3	..	..
November	3	0	6	4	7	3	..	..
December	5	0	9	3	6	3	..	..

Curves were drawn for all species caught in sufficient numbers. The tables are used for the discussion of some of the less numerous fishes. Several species were not caught often enough for continuous tables or curves and are excluded. Catch records for the rarer fishes have been given by Gunter (1935). The hauls were divided into inside and outside groups and corresponding tables and curves made. The differences between inside (bay) and outside (gulf) waters are sharp enough to warrant such a division. Each species is treated individually.

SEASONAL VARIATIONS IN ABUNDANCE

Seasonal variations were among the first phenomena of life that man noted. The particular variation under consideration here is one of abundance, and is related to numerous other variations or cycles, such as spawning, migrations, variations of food, the cycles of seasons, and abundances in other animals in a number of known and unknown ways.

One of the first questions that arises is what causes seasonal changes in animal numbers? Why should a fish which seems to be more or less homogeneously distributed over an area suddenly become ten or a hundred times more numerous than before? Most animals have definite seasonal breeding periods within each year. These reproductive cycles bring about annual variations in numbers of the total population. Holding in mind that the method of detection used here is abundance in trawl catches in one locality, it is plain that these peaks may be seemingly caused or made apparent by two things: (1) An influx of young which were hatched and raised in the region, and which have attained size enough to be taken in the trawl (as was indicated above this is not at all large), or (2) A migration of young or old individuals from another locality. The young may be migrating to or from nursery grounds. The older animals may be moving to or from spawning grounds, or on a seasonal migration brought about by changes in the environment. The

real causes of abundance peaks are many known and unknown antecedent factors, some of which will be discussed below for the various species concerned. Consideration must also be given to the possibility that the abundance peaks are fortuitous, or in other words are brought about by inadequate sampling of the population. Nevertheless, the regularity of several of the curves, recurring seasonal modes and the similarity of the curves for the fishes of the order *Heterosomata* indicate that sampling was adequate.

Since most of the data are presented in the form of curves the terms used in describing the variations in numbers of the various fishes will be those of a simple statistical curve.

It is implied in speaking of seasonal variations in abundance that they are more or less cyclic or rhythmical in nature, recurring from year to year. Flattely (1920) has pointed out that there are two types of biological rhythm, (1) those correlated with the environment and (2) those inherent in the organism, the latter being probably correlated with the age cycle. Several workers have shown that animals in the tropics have definite breeding rhythms, although the seasonal differences are very slight or none. The work of Yonge (1930) on the Great Barrier Reef is an example.

Pearse (1926) summarizes the matter in these words: "The annual cycle of many species of animals is made up of a series of stages in a characteristic life history or of a characteristic series of periods of rest and activity which are closely correlated with seasonal succession. Long established correlations operate in such a way that seasonal environmental changes serve to stimulate animals to appropriate activities or inactivities and cyclical physiological changes within animals prepare them to react properly with recurring seasonal events."

Elton (1927) states that: "The numbers of very few animals remain constant for any great length of time, and our ideas of the workings of an animal community must therefore be adjusted to include this fact."

Before going further it is well to call attention to Verworn's (1913) pertinent criticism of the word *cause* as often used by workers in science and others. He points out that the happening of any event is preceded by an infinite concatenation of antecedent factors, the removing of any of which would preclude the happening of the event. He further points out that the seizing upon of any one of these conditioning factors and calling it a cause in contradistinction to the other factors which are of equal value in conditioning the given event is an improper and false usage. This is especially the case in ecological work where there are so many interrelationships seen and unseen. Nevertheless, the usage of the word *cause* is so common and ingrained in the language that it will be used with the above reservations in mind.

A complete answer to the many questions arising from the data would entail a complete study of the biotic associations of the whole area. The difficulty of attainment of this ideal have been pointed out by Elton (1927).

whose remarks relate to succession, but are applicable and are quoted here, ". . . it is almost impossible to make even a superficial study of succession in any large and complicated community, owing to the appalling amount of mere collecting which is required, and the trouble of getting the collected material identified. When one has to include seasonal changes throughout the year as well, the work becomes first of all disheartening, then terrific and finally impossible." Elton then counsels that the ecologist choose simple communities for they are just as valuable for purposes of theory. This, of course, is of little satisfaction to the marine ecologist or fisheries zoologist, who of necessity must work in a given area where particular species reside and which is never simple.

In the face of the impossibility of working out the problem as a whole, a given set of phenomena such as seasonal variations in abundance must be selected and as many legitimate conclusions drawn from them as possible. It seems very probable that only by such forward inching movements will the life histories of fishes and their interrelationships with their environment be worked out.

SCIAENIDAE

An understanding of the vastness of animal numbers and the numerical relationships of the various species or groups will probably often result in changed viewpoints. Elton (1927) has pointed out the interesting censuses of soil fauna at the Rothamsted Experimental Station, where it was found that the generally neglected springtails were more numerous than the flies and about seventy-eight times as numerous as the lepidoptera.

Censuses of fishes in a large area are very difficult and probably will always be relative. However, data have been presented (Gunter, 1938) which indicate that the *Sciaenidae* is one of the most successful families in this area from a numerical standpoint.

Micropogon undulatus (Linnaeus)

The croaker is the most abundant fish in trawl catches on the Louisiana coast. It is numerous at all times and at certain seasons its numbers are enormous. Millions are caught every year by shrimp trawlers.

Figure 2 shows that in 1932 there was a summer maximum abundance for this species on the inside extending from May to September with a mode in June. In 1933 it came earlier and did not last as long. The fish taken on the inside were small to medium-sized and grew rapidly as the summer progressed. On August 1, 1932, croakers taken on the inside ranged from 7.8 to 12.0 cm. in length. During the middle of October they ranged from 9.0 cm. to 13.5 cm. in length. On July 31, 1932, croakers caught on the outside ranged from 9.0 to 13.2 cm. in length while in the middle of October they varied from 8.5 to 17.5 cm. In the open gulf, as shown by the curve, there was a summer plurimum extending from May to October in 1932 with a peak

in September. The two curves rise and fall reciprocally in the summer of 1932 and from May to July in 1933.

It is evident that the fish pass to the outside as they grow larger. They do not return to the bay in winter and probably go out to deeper water. Pearson (1929) stated from general observations that there is a noticeable migration of croakers from the bays to the gulf in September. The curves here for 1932 show this and in 1933 the migration came earlier. The chief spawning month is in November according to Pearson and it seems that as the fish grow up they migrate to the gulf and congregate in preparation for spawning.

Post-larval and very small specimens occur in the bay in the winter and are abundant in February and March. Pearson has taken them from October to February in Texas, which indicates a long spawning season. The young and post-larval forms were never taken except in the bay and most abundantly in the headwaters. Pearson has shown that the croaker spawns on the outside near the passes and has observed the young making their way into the bay in large schools. The very young have been taken fifteen miles offshore in nets at Beaufort, North Carolina (Hildebrand and Cable, 1930) and it is probable that they spend some time in the plankton before starting inshore.

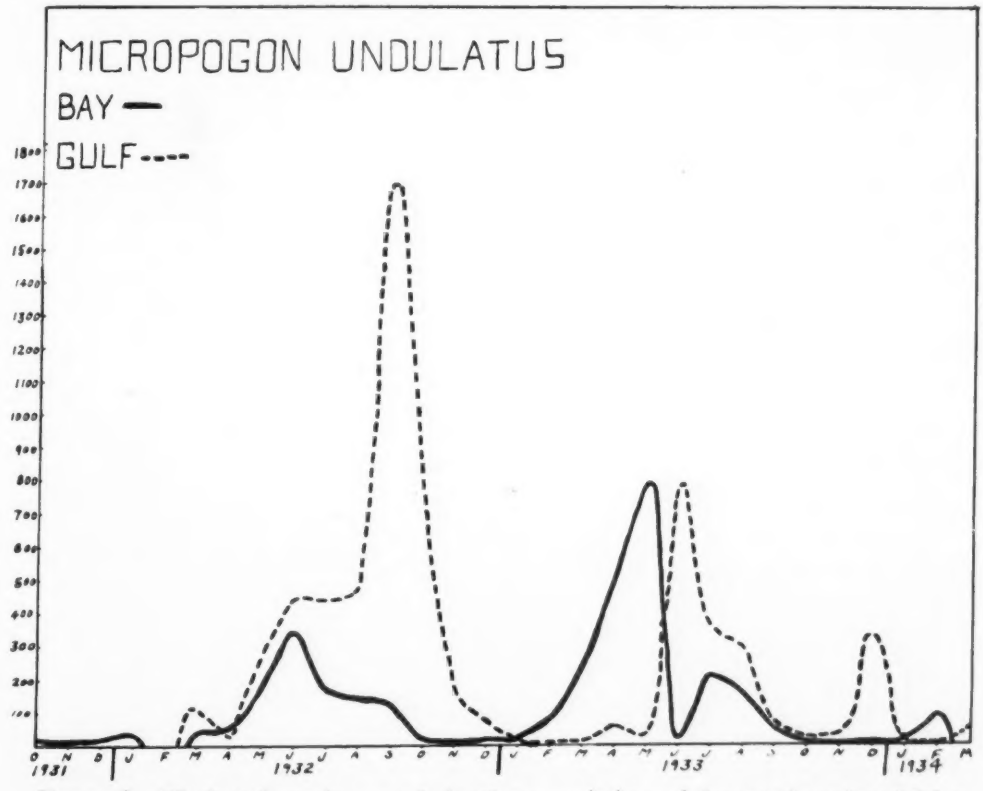

FIGURE 2. All plotted graphs are of abundance variations of the stated species of fishes, as determined by the catch in otter trawls from October, 1931 to March, 1934. The months and years are given along the x-axis. The figures along the y-axis are the average number of fish caught per haul each month. Separate curves for the bay (—) and gulf (---) waters are shown.

In the trawls only the largest animals were taken at this distance from the shore.

It is interesting to note that during the winter and early spring the water in the upper part of Barataria Bay becomes very fresh. The young seem to be more cold-resistant than the older fish for they are caught in the late winter in shallow water when the latter are offshore in deeper water. This phenomenon has been noted before for the croaker and the spot by Hildebrand and Cable.

Stellifer lanceolatus (Holbrook)

This fish ranks next to the croaker in numbers in trawl catches. It is very small and does not grow much larger than 12 cm. in length. It is of no commercial importance, but is probably of great ecological importance in the animal associations of this area.

Fish of this species seem to prefer the shore waters of the open gulf, for they were seldom taken in large numbers far from land and were usually scarce on the inside except in September, 1932, and July and October, 1933. This time also corresponds to the greatest abundance in the gulf for these years.

There was a peak of abundance on the outside in the summer of 1932 and 1933 as shown by Figure 3. Animals ripe enough for stripping were taken in April, May and June, 1933, and as the animals taken at this time are adult it is possible that this abundance is due to congregating of breeding individuals. Welsh and Breder (1923) say that May and June are the principal spawning months on the Atlantic coast. The post-larval and small animals come into the fishery to maintain the peak noted in late summer for both the inside and outside. These grow rapidly during the summer and fall. Welsh and Breder state that maturity is reached in one year, and also say that the largest fish they observed was two and one-half years old.

The writer's observations, which unfortunately are not checked by adequate total length measurements, were that many of the larger animals disappear after spawning and it seems that this fish has a short life cycle. Scale readings and total length measurements will determine the point. Pearson (1929) states that the related species, *Micropogon undulatus*, spawns for the first time in the second year and that few appear to live after that. Two fish taken on August 1, 1932, in the bay measured 8.0 and 10.3 cm. respectively. Seventy fish taken in the gulf in October ranged from 5.0 to 12.0 cm. in length and most of them were below 10.0 cm.

Menticirrhus americanus (Linnaeus)

The figure (4) for the black mullet shows a very slight peak in numbers on the inside in September and October in 1932, and October and November in 1933. It is clear that the numbers of this species fluctuate in the gulf, but the figure shows that they reach a maximum in the winter. There is a small

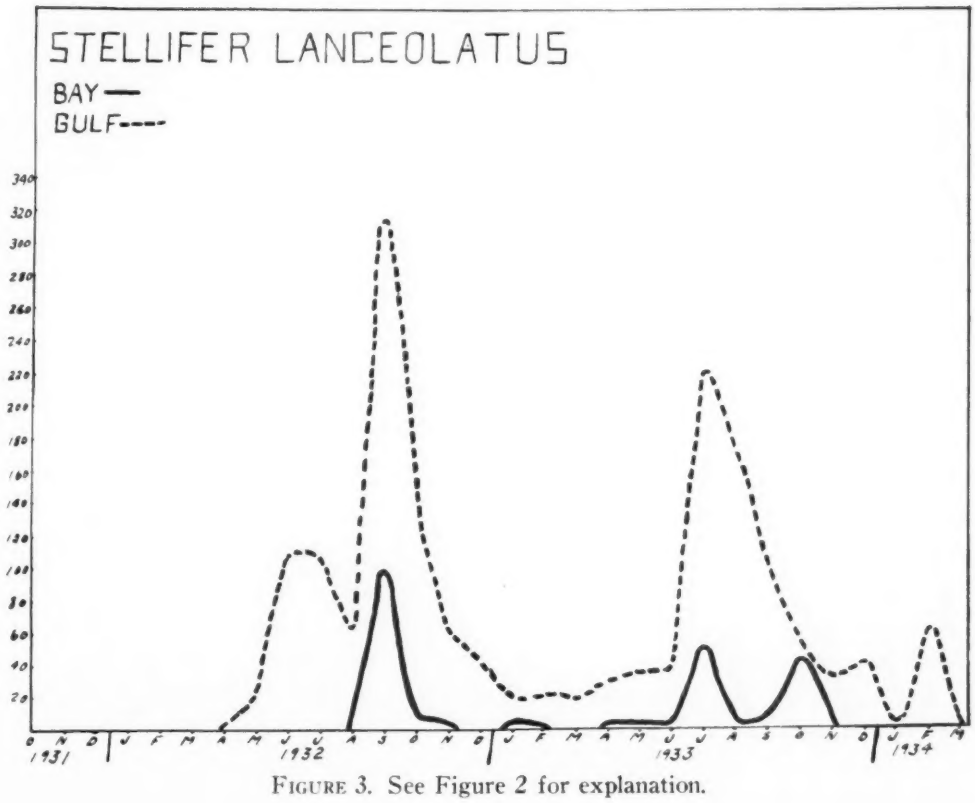

FIGURE 3. See Figure 2 for explanation.

peak in September and October of 1932 corresponding with that on the inside. The time of greatest abundance was in February and March, 1933, on the outside. Fish with well-developed roe were taken in April, May and June, 1933, in the gulf. Smith (1907) states that *Menticirrhus americanus* spawns in June at Beaufort, North Carolina. Hildebrand and Cable (1934) state that the season at Beaufort is from April to August or September and that fish with well-developed roe are most common in May and June. Smith also states that the species is most abundant in the spring and is present in schools in the fall. This corresponds with the findings in Louisiana which show the black mullet is most common from September to March. The curves also show clearly that the fish prefers gulf waters.

Bairdiella chrysura (Lacépède)

The yellowtail, as shown in Figure 5, fluctuated in numbers in the gulf and was not common. In January, 1932, there was a marked peak of abundance in Barataria Bay. The following year this was not the case, but in January, 1934, the mode was repeated on a smaller scale. The explanation for this is not known. There is a slight peak on the inside in August, 1932, and a large one during July of the next year. These modes may have been due to the migration of fish after spawning.

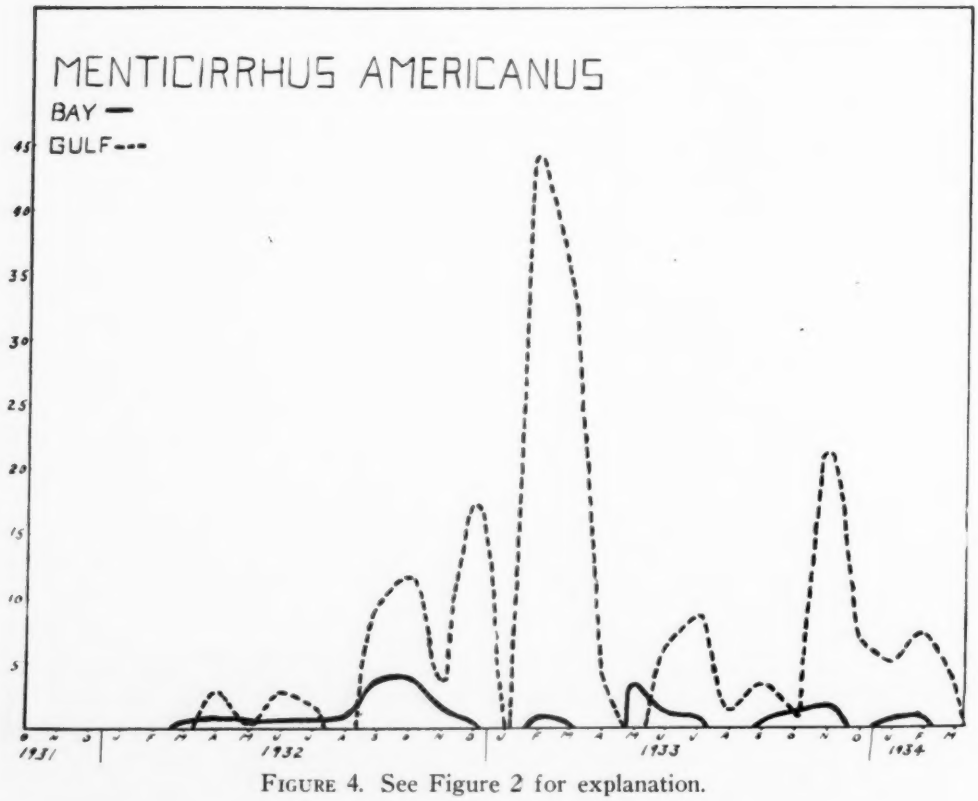

FIGURE 4. See Figure 2 for explanation.

Females ripe enough for stripping were taken in April, May and June, 1933, both in the bay and in the gulf, which agrees with the statements of Hildebrand and Cable (1930) that the spawning season is from the end of April to the end of June at Beaufort. The peak on the inside was made by small individuals which probably developed from this spawning. Unfortunately very few measurements were made. Four fish taken in the bay on August 1, 1932, measured between 8.3 and 9.0 cm. in length. Thirty-eight fish taken from 2 to 3 miles out in the gulf on July 31 of the same year measured from 10.2 to 13.3 cm. in length. Twelve fish taken in the bay from October 14 to 16, 1932, ranged from 9.0 to 12.0 cm. in length.

Hildebrand and Cable (1930) found that *Bairdiella chrysura* grows amply large enough to sexually mature at the age of one year, although it is not actually known that it spawns at this age. Probably the life history is short and somewhat like that suggested for *Stellifer lanceolatus*.

Leiostomus xanthurus (Lacépède)

Figure 6 shows that there was a decided abundance mode of this species in the gulf during June and July, 1932, with a slighter peak at the same time on the inside. The increase in numbers first began in the gulf in April, 1933, instead of May as in 1932. It roughly corresponds to the mode of the latter

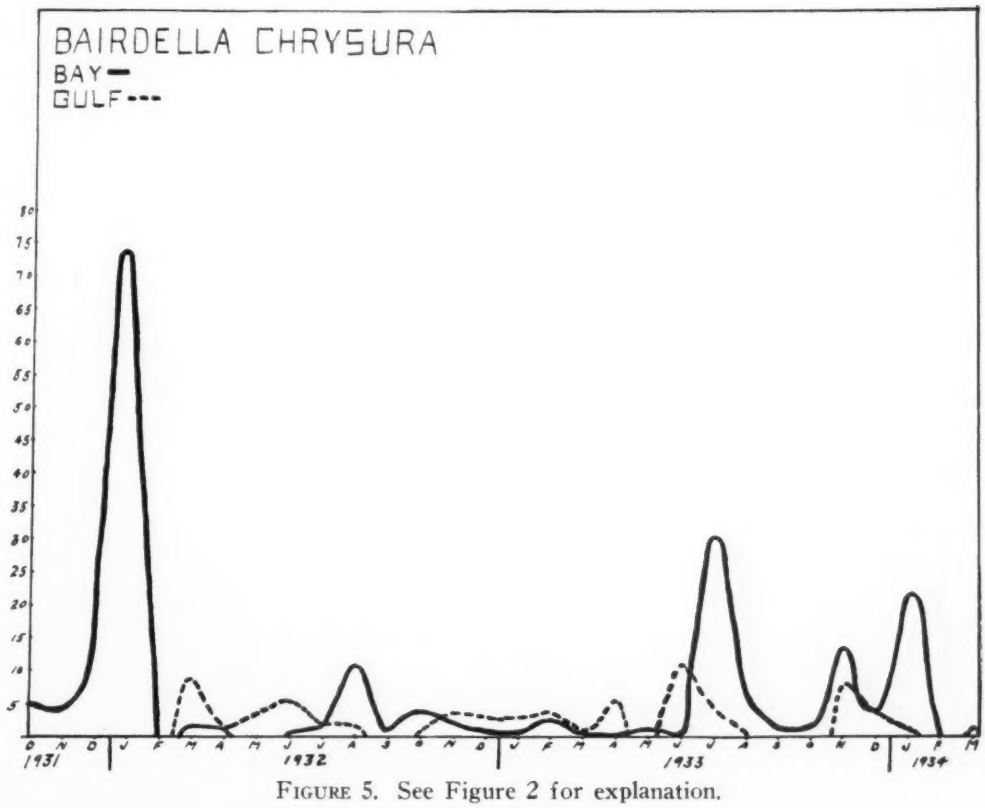

FIGURE 5. See Figure 2 for explanation.

year except that it is a little longer and the abundance is most pronounced on the inside and in August rather than in June as in 1932. The fish is probably adapted to both environments but is sensitive to changes or has "preferences," so that the greatest numbers may be in the gulf in one summer and in the bay during another, depending on unknown factors.

The individuals making up the summer abundance peak first appeared in the gulf. They were from 2.5 to 3.5 cm. in length and had evidently been spawned a few months before. Pearson (1929) states that in Texas the spot spawns from late December to the last of March with the height of the season in January and February. Possibly the peak noted in January, 1934, was made by spawning fish. It was not seen in other years.

The young fish grew rapidly and appeared to attain adult size by the end of the summer, when their numbers began to decline. Pearson (1929) noted this rapid growth in Texas. In Louisiana forty specimens taken in the bay in August, 1932, measured from 9.5 to 13.5 cm. in length. Sixty fish taken from the bay in October, 1932, measured from 11.0 to 16.0 cm. in length.

The curve shows that just before each summer increase in numbers the spot entirely disappears. This agrees with the statement of Pearson that after the first spawning most of the fish apparently perish. The disappearance noted may be explained on the hypothesis that adults died after spawning and

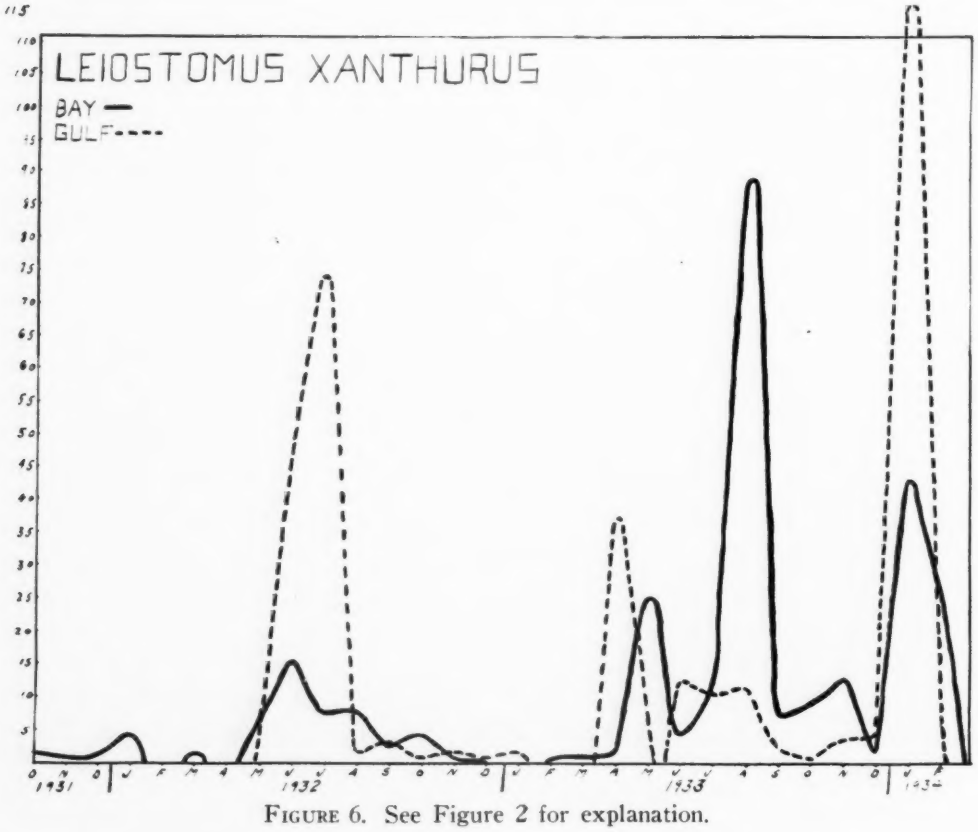

FIGURE 6. See Figure 2 for explanation.

the young are not immediately taken in the trawls because of their small size. Apparently the life cycle of *Leiostomus xanthurus* is short.

Larimus fasciatus (Holbrook)

Table 1 shows that the banded croaker was rarely caught in inside waters. Hildebrand and Cable (1934) state that they have no record of it entering the harbor or sound at Beaufort, N. C. In the gulf there was a slight increase in numbers in August, 1932. The same small increase was present in August, 1933. Hildebrand and Cable say that spawning takes place over the whole summer and begins as early as May at Beaufort. Post-larval animals were taken in seine hauls on the beaches in Louisiana during May, 1933, and it is possible that spawning begins here a little earlier, probably in April.

This fish is one of the smallest sciaenids, and unlike most members of the family in American waters is of no commercial importance. The total numbers at the time of greatest abundance were not large, but as the fish is relatively scarce at all times they are as marked as the greater increases are for more common species. The summer abundance is probably due to the fact that the young of the year attain size enough to be taken in the trawls at that time. Five individuals taken in the gulf in October measured from

12.0 to 14.0 cm. in length. According to Hildebrand and Cable some of the young of the O class attain a length of 7.0 cm. by July at Beaufort.

Welsh and Breder (1923) indicate that this species is one of the most abundant on the shores of the Gulf of Mexico. The statement probably applies to Florida, for it is not true of Louisiana.

OTOLITHIDAE

Cynoscion arenarius Ginsburg

The curve for the white trout on the inside, pictured in Figure 7, shows a wide mode from June to October which fluctuates strongly from month to month in 1932. As cooler weather approaches most of the fish depart for the open gulf. This fluctuation may be due to a back and forth movement from one part of the bay to the other or more likely from the inside to the gulf. This movement may be due to a sensitivity to some environmental condition. An analysis of hydrographic data collected at the time of this study may shed more light on the subject. In the winter of 1932 the fish were numerous in the gulf although not so much as in June and July. In the winter of 1933 there was a marked mode with a peak in December which exceeded the summer peak on the outside for that year with the high point in August. There is also a marked fluctuation on the outside in winter.

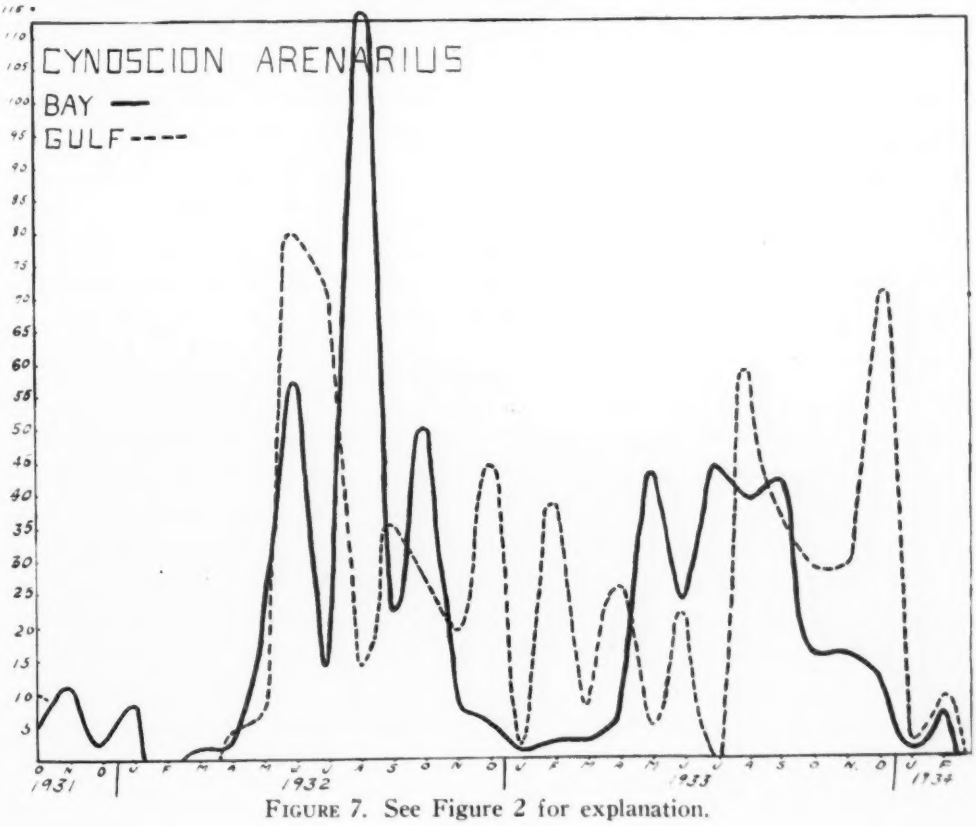

FIGURE 7. See Figure 2 for explanation.

Higgins and Pearson (1927) state that the height of the spawning season for *Cynoscion regalis* is reached in June in North Carolina and that season is over by August 10. *C. arenarius* with well-developed roe were taken in Louisiana in April, May and June of 1933. It seems that the spawning season for the two species corresponds roughly and it is possible that the high peak of abundance in June and July of 1932 in the gulf was due to breeding animals.

Small fish were taken in large numbers during the fall in inside waters. As the fish grew up they passed into the gulf. This is shown by the fact that the inside curve for winter months drops almost to the base line. In August, 1932, eighty-seven fish from the bay measured from 7.5 to 14.0 cm. in length. In October 117 fish taken in the same place ranged from 5.0 to 15.0 cm. in length, while forty from the outside measured from 10.5 cm. to 20.0 cm. in length.

Cynoscion nothus (Holbrook)

Cynoscion nothus is a smaller species than *C. arenarius* and frequented the gulf almost solely. Its abundance increased directly as the distance offshore up to six or eight miles. The reverse is true of the latter fish for it was more common in the bay. Eighteen hauls made in the summer of 1933 one mile offshore gave 62 *C. nothus* while 18 hauls made on the same days, three to six miles offshore gave 223 fish. Ginsburg (1931) has previously called attention to this distributional difference of the two species. *C. nothus* was taken in the bay during the months of December, 1932, and January and May, 1933. In all probability it is sensitive to temperature rather than salinity, like the mackerel in the Black Sea as observed by Galtsoff (1924). It is to be noted that the salinity of the bay at this time of the year is much lower than that of the fish's usual habitat. Table 2 shows a summer peak of abundance on the outside in August, 1932, and July and August in 1933, somewhat like *C. arenarius*. It was not as common as the latter fish.

Cynoscion nebulosus (Cuvier and Valenciennes)

Unlike the preceding species the largest specimens of *C. nebulosus* were not taken in the trawls. Smaller fish from 2.5 to 20.0 cm. were often taken on the inside. Higgins and Lord (1926) quote fishermen as saying that spotted trout are most common in December, January, February and March in Texas, which agrees with the findings in Louisiana. They also quote notes of Simmonds, saying that the fish spawn from May to early September. Pearson (1929) states that the spawning season extends from March to October and the height of the season is reached in April and May in Texas. He also shows that spawning takes place in inside waters. Two large females with hard roe were taken by the writer at the mouth of Barataria Pass in the latter part of May, 1933.

In Louisiana (Figure 8) a few stragglers were taken in the gulf in March, 1932, and again in January and February, 1933. Smaller individuals, if not adults as well, prefer inside waters. A marked increase in numbers was found in the winter with January as the peak month in 1932 and 1933. February was the month of greatest abundance in 1934. These modes were caused mostly by small fish which obviously were spawned the previous spring and summer, although other sizes were not uncommon. There was much overlapping of various sizes which Pearson (1929) says is due to a protracted spawning season, making it difficult to sharply identify year classes. Like the croaker the young of this fish were found to be very tolerant of freshwater and low temperatures. Numbers increased from the mouth to the headwaters of the bay, where they attained a maximum and at times predominated in the catches, even exceeding the ubiquitous croaker. Likewise, larger specimens were taken nearer the gulf, but never in as great numbers.

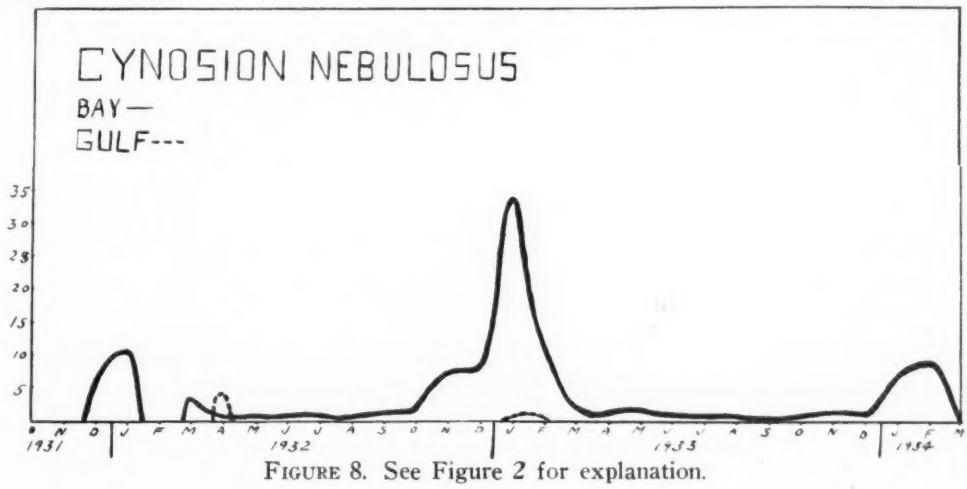

FIGURE 8. See Figure 2 for explanation.

POLYNEMIDAE

Polynemus octonemus (Girard)

In 1932 the threadfin appeared in May both in the bay and the gulf as shown by Figure 9. In April, 1933, it was first taken in plankton tows in the gulf. The fish were then about 5 cm. in length. They grew rapidly and were about twice that size by the end of the summer. This species is only a summer and fall resident and its arrivals and departures were as regular as those of migratory birds. The figure shows that it left the area studied in October in the years 1932 and 1933. The period of residence is from April or May to October. The 1933 abundance in the bay was due to large schools of small fish which were often observed and caught in dip nets at night, near the electric lights of a shrimp platform.

Piecing together the story from the facts at hand, it seems that the young which were spawned the previous fall or winter first appeared offshore in the

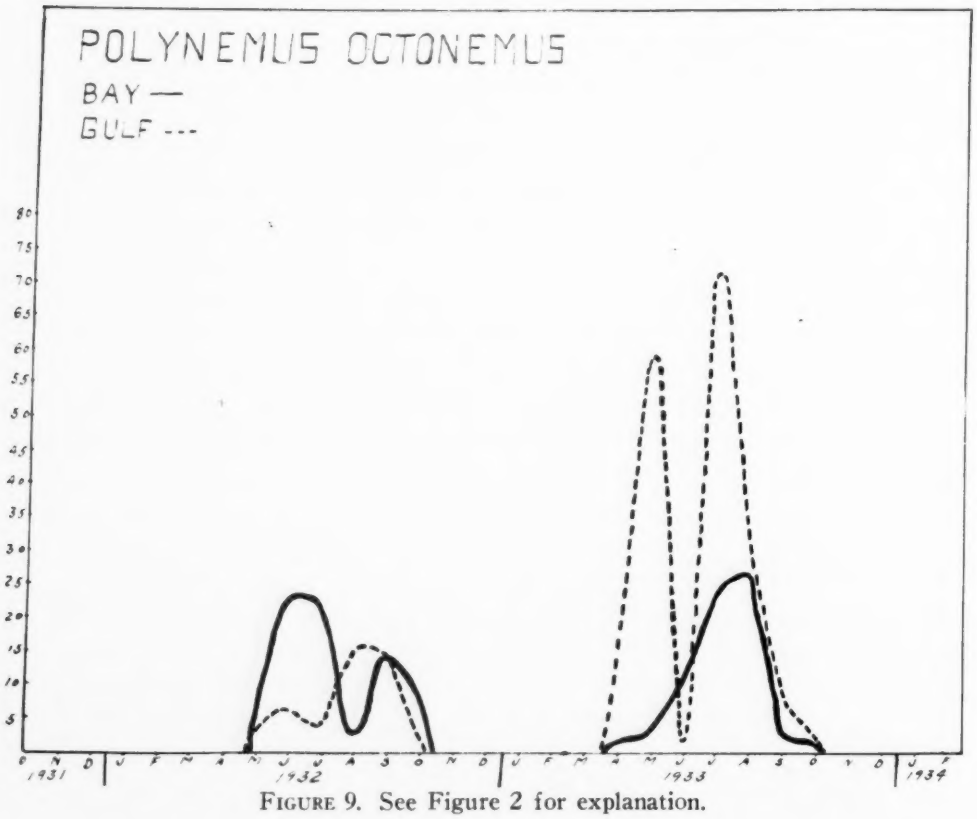

FIGURE 9. See Figure 2 for explanation.

spring and came into the bay forming the summer abundance peak noted for two consecutive years. Here they grew rapidly and returned to deeper water in the fall. Ninety-one fish taken in Barataria Bay in August, 1933, ranged from 7.8 to 13.5 cm. in length. Four fish taken there in October measured from 11.5 to 13.0 cm. in length, while fourteen fish taken in the gulf at the same time ranged from 13.0 to 15.0 cm. in length. Whether this species spawns close to shore or in deep water is unknown, but the latter supposition is the more probable. At any rate, the young were not caught until the following spring.

TRICHIURIDAE

Trichiurus lepturus (Linnaeus)

Figure 10 shows a summer peak of abundance for the cutlass fish in the gulf, beginning in April in 1932 and in July, 1933, with both extending through September. There is also a smaller peak in the winter extending from November to March or April for both 1932 and 1933. The curve fluctuates but is similar for the two years. In 1932 the fish was not plentiful in the bay, but compared to its winter population of that and the year before it was at a peak paralleling that on the outside for the same time. In 1933 this peak was well apparent and extended from May to October.

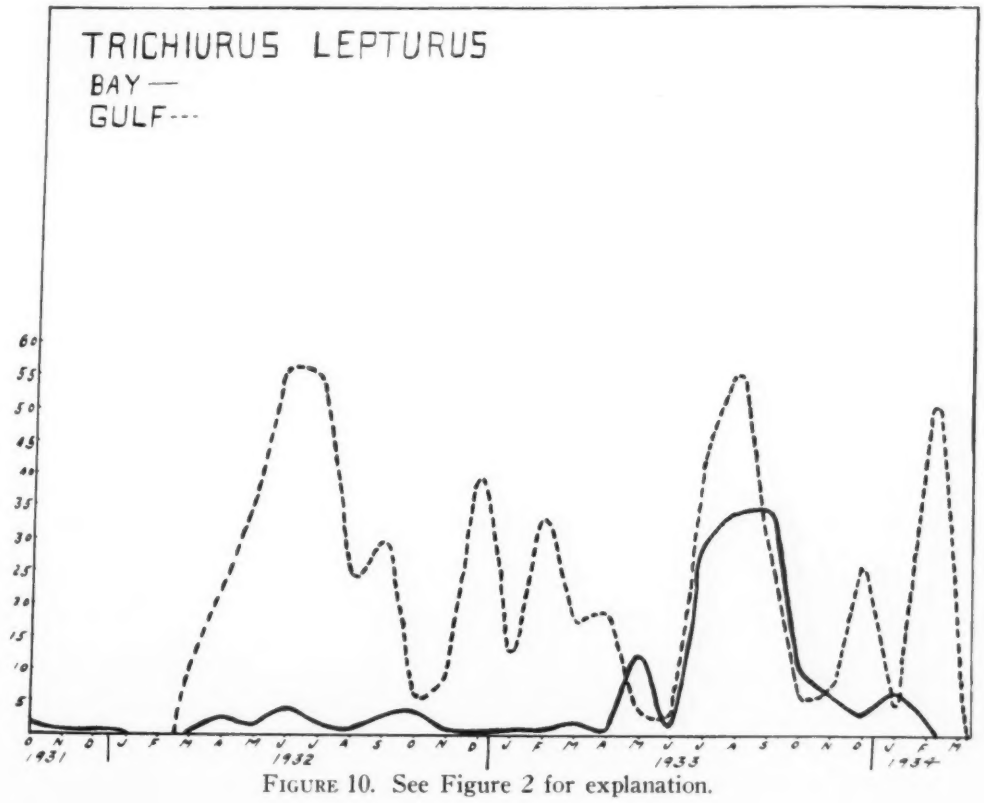

FIGURE 10. See Figure 2 for explanation.

Smith (1907) states that spawning takes place in the summer, for a ripe fish was taken at Beaufort in August. In the last week of April, 1933, the very attenuated young first appeared in the catches in the gulf. Perhaps they were spawned in the previous summer or fall. No measurements were made but general observation indicated that they composed most of the catch on the inside for that year. The peak began in May immediately after the first appearance of the young. In the bay they preponderated, but size limits were very wide in both localities and it is probable that several year classes were present. It is evident from the figure and observations here related that the young are probably spawned on the outside, pass to the bay nursery grounds during the summer and return to the gulf in the fall. The winter modes were at peaks in December and February for two consecutive winters. This fish is more common in the gulf than in the bay, contrary to the figures given by Gunter (1938) where those for the outside are erroneous.

STROMATEIDAE

Poronotus triacanthus (Peck)

The butterfish was never taken in large numbers. It seemed to prefer gulf waters and when caught in the bay was more plentiful near the lower end. In the late winter and spring of 1933 it was much more plentiful than in the

preceding year (Table 2). This group was composed chiefly of half-grown fish. The period of abundance in the gulf extended from February to June. The previous year and the following year this numerical increase was not noted, so it cannot be said whether or not it is typical of the life cycle.

CARANGIDAE

Caranx hippos (Linnaeus)

Table 2 shows that the jackfish was caught in small numbers in the bay from July to September in 1932 and July to November in 1933. On the outside it was most common in the summer months with an occasional straggler in spring and fall. All specimens taken were of small size, the largest not exceeding 15 cm. in length. Very often the small fish were taken from the bell of the jellyfish, *Stomolophus* sp. Adult fish were common in the summer three or four miles offshore. In the winter they were absent and evidently passed out to deeper water.

Selene vomer (Linnaeus)

Table 1 shows that the lookdown was not caught in the bay at all. It was absent from the gulf in winter at the points visited. Its appearances were sporadic, though in October, 1931, and September, 1932, it became plentiful. There may be an abundance peak at this time which cannot be detected due to the fish's sporadic appearances. Hildebrand and Schroeder (1928) observed this species in Chesapeake Bay only in September and October.

Vomer setapinnis (Mitchill)

Figure 11 shows that in October, 1931, and in September, 1932, and October, 1933, the moonfish was numerous inside. Hildebrand and Schroeder (1928) observed that this species was most common in Chesapeake Bay in September and October. The figure also shows that the fish was absent from the bay in the winter and spring. This is the season of low temperature and salinity. Fish taken in the bay were of all sizes and the numbers cannot be attributed to a migration or sudden appearance of the young. This species frequents the open gulf, and it seems that the increased catch at this time is a result of a general ingress to the bay at a season when the water conditions are suitable and comparable to those of the inshore gulf. The fish was always more common at the lower end of the bay. The curve for the gulf shows a rise in numbers in March, 1933. Beginning in July there is a mode with a peak during October. There is a peak on the inside at the same time. Then the fish depart for deeper water. It is clear that this species is most numerous in the fall. Yarrow (1874) recorded the fact at Beaufort, North Carolina, many years ago.

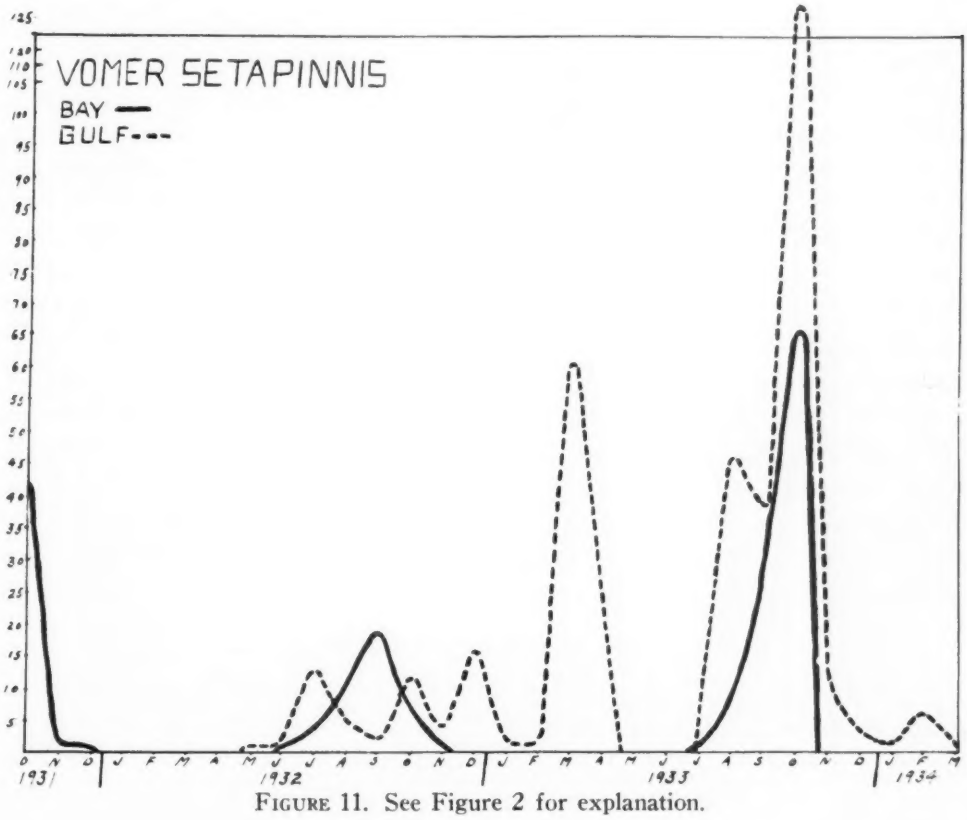

FIGURE 11. See Figure 2 for explanation.

Chloroscombrus chrysurus (Linnaeus)

The bumper was taken in the bay in October, 1931, and August, September and October in 1932. Like *Vomer setapinnis* it was caught near the lower end of the bay at a season when the hydrographic conditions were comparable to those of the shallow water of the gulf. At all other times it was absent. Table 2 shows that the animal was taken chiefly in the fall in the gulf. There seems to be a peak of abundance at this time. It was quite common in March, 1933, although it was not found the preceding or following month. This may have been due to migration along the coast.

CLUPEIDAE

Brevoortia patronus (Goode)

The menhaden is quite common and is possibly more numerous than trawl catches indicate for it is a plankton feeder and not as susceptible to capture as bottom feeding fishes. The writer has observed large schools feeding near the surface in Caminada Bay where they wheeled, turned and swerved from side to side in perfect unison, all the while with mouths agape and lower jaws thrust forward.

Figure 12 shows that this fish was caught much more in the bay than outside. Individuals from inside were mostly immature and it is possible that

adults were present in larger numbers in the gulf. During the months of June and July in 1932 and June, 1933, the menhaden was scarce inside and was taken more commonly in the gulf. In 1932 there was a peak in the bay in January. The following year the peak came in December and January and in 1934 it came in January and February. This is ample data to establish the fact that there is an abundance peak for this fish in the bay during the winter, which is characteristic of the life history of the species. The winter mode was made up of small fish which must have been spawned the previous summer and fall. Smith (1907) records that large schools of young *Brevoortia tyrannus* are present from December to March near Beaufort. Hildebrand and Schroeder (1928) say that *Brevoortia tyrannus* seems to hatch in the fall in Chesapeake Bay. The increased numbers caught in midwinter, indicated in Figure 12, are possibly a result of migration of such individuals from nursery grounds near the shore to the open bay. They grow rapidly and probably by midsummer most of them pass to the outside, as the curves indicate. Fish taken on the outside were usually adult or nearly adult in size. Smaller individuals were sometimes caught near the shore.

Signalosa atchafalayae (Evermann and Kendall)

As shown by Tables 1 and 2 this fish was occasionally taken in the gulf, although most of the time it was completely absent. Like the menhaden it was

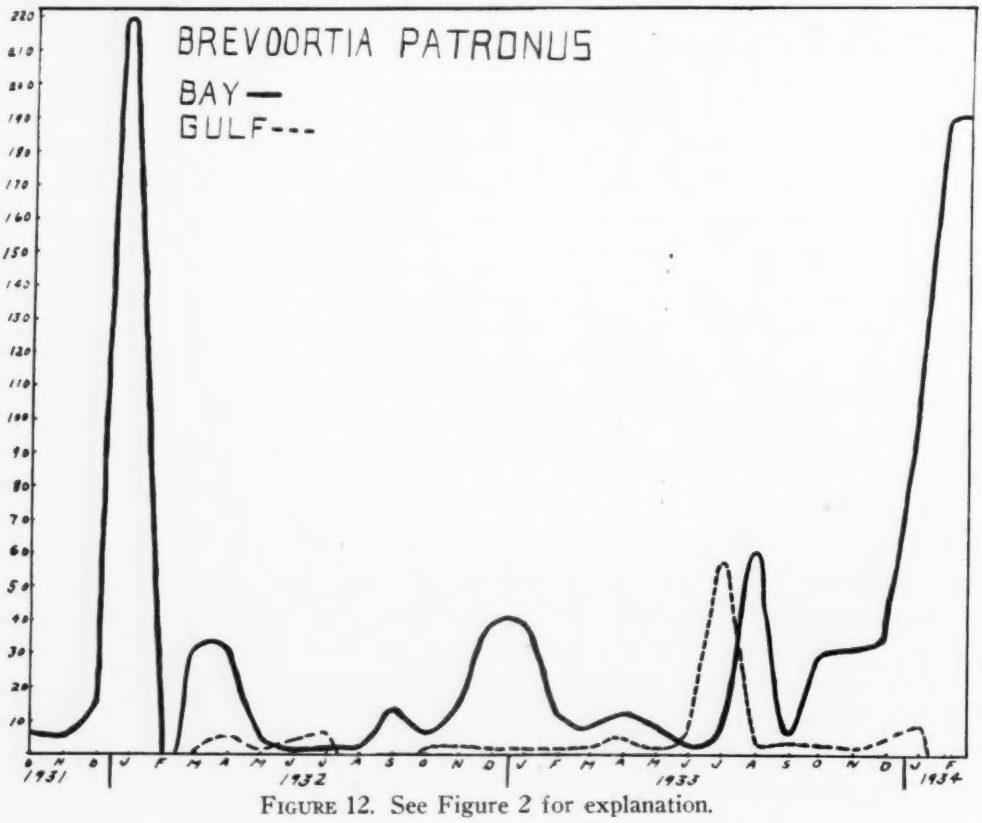

FIGURE 12. See Figure 2 for explanation.

taken most often in bay waters. In 1932 it was abundant in December. In the previous year it was more numerous in January; in 1934, in January and February. There was also a slight increase in numbers in the fall of 1933, as in 1932. The fish taken in midwinter were mostly small and were probably spawned the summer before. The seasonal variation in numbers for this species is much like that of its relative, *Brevoortia patronus,* previously described.

ENGRAULIDAE

Anchoviella epsetus (Bonnaterre)

Anchovies were very common, but relatively few were caught in the trawl because of their small size. On numerous occasions the writer has seen them thrown into the water in hundreds by a slight shake of the net. They probably have a prolonged spawning season during the summer and fall, for the young appear by millions in the late winter and spring. Hildebrand and Cable (1930) state that the spawning season at Beaufort, N. C., is from May to August. Specimens with well-developed ovaries were taken in the gulf in May.

In 1932 (Figure 13) the fish were very numerous on the inside from December to May with the peak in April. Almost all were small. On the outside the mode extended from March to June with the peak in May. The

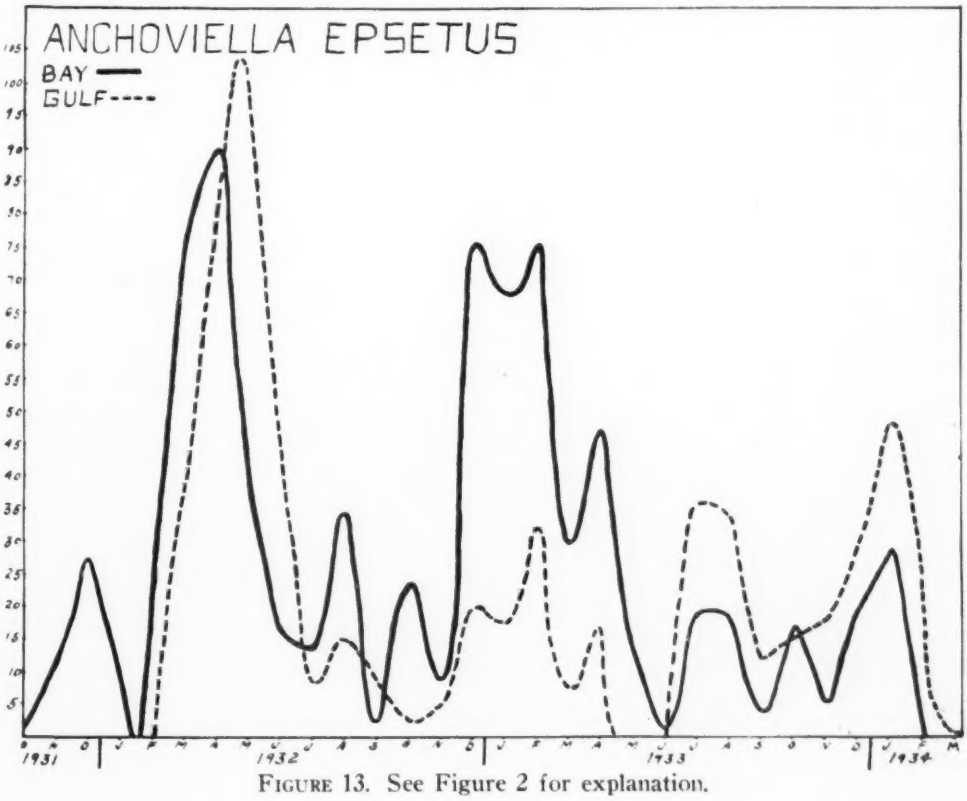

FIGURE 13. See Figure 2 for explanation.

two following years there was a peak in both the bay and gulf in midwinter which declined in March in 1933 and February, 1934. Small post-larval fish make up the winter abundance. Larger fish make up the summer population. Post-larval anchovies were taken in large numbers in the bay, while in the gulf they were taken more rarely. The fish caught in the open sea were of larger size than those of bay waters. They probably spawn in the gulf in shallow water. It was seldom that adults were taken on the inside. During the summer of 1932, 216 fish from the bay measured from 3.5 to 10.5 cm. in length while 26 from the gulf ranged from 4.4 to 11.5 cm. in length.

ARIIDAE

Bagre marinus (Mitchill)

Figure 14 shows that the gaff-topsail catfish was abundant in September, 1932 and 1933, both inside and outside. The curve for the hardhead catfish, *Galeichthys felis,* shows the same picture except that in 1933 the peak was in October for the inside with a high point in July for the outside. In both species this inside peak was made to a large extent by small fish, which were carried about as eggs and hatched in their father's mouths during the summer.

Males of both species carrying eggs were first taken in Barataria Bay the 12th day of June in the 1933 season. At the same time large schools of

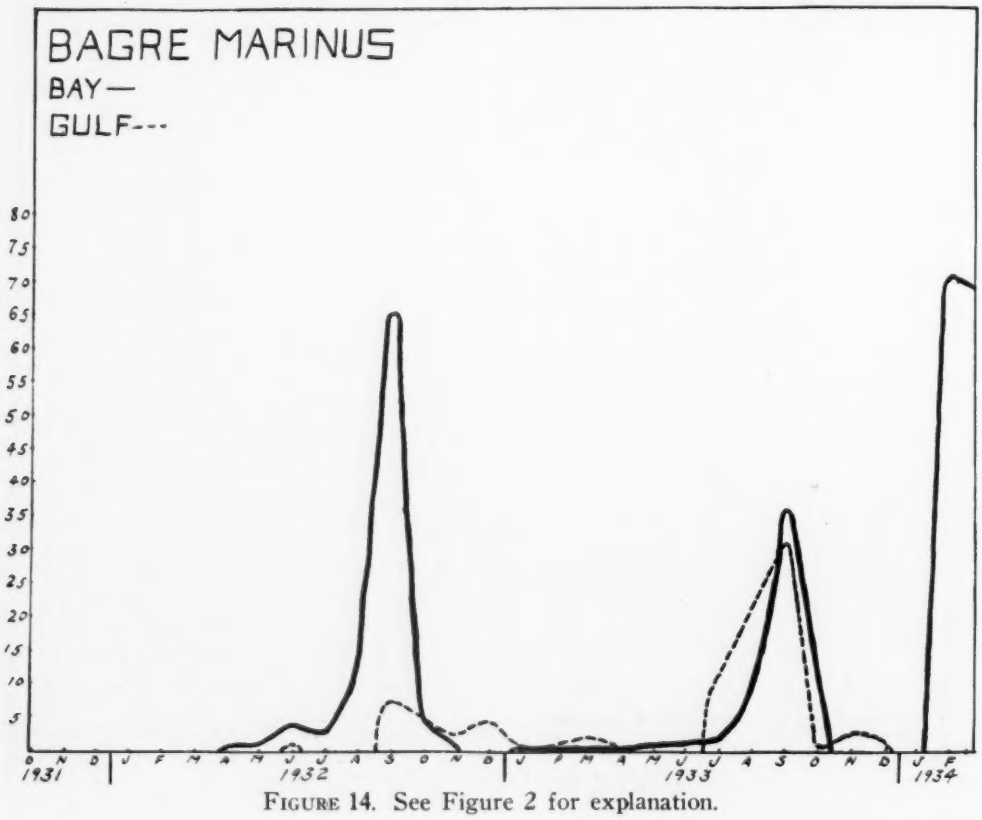

FIGURE 14. See Figure 2 for explanation.

"hardheads" were reported to be "breeding" in Caminada Bay. The writer did not observe these schools but saw fish caught there at that time, which had eggs in their mouths. No fish which were carrying eggs were caught in the gulf. This is similar to the case of *Galeichthys felis* (Lee, 1937). The figure shows that after September most of the fish went to the gulf. They returned again to the bay the next May and June prior to spawning. February, 1934, is an exception.

Galeichthys felis (Linnaeus)

The hardhead is more common than its close relative, the gaff-topsail. The abundance peaks for September, 1932, and October, 1933, have been discussed with those for the former catfish. These fish very often go in schools and evidently move about quite a bit. A number of *Galeichthys felis* spend the winter in the bay (Figure 15). This is contrary to the case of *Bagre marinus*.

GADIDAE

Urophycis floridanus (Bean and Dresel)

Tables 1 and 2 show that this species was present in March and April, 1932. It was present from January to March in the gulf in 1933, and from

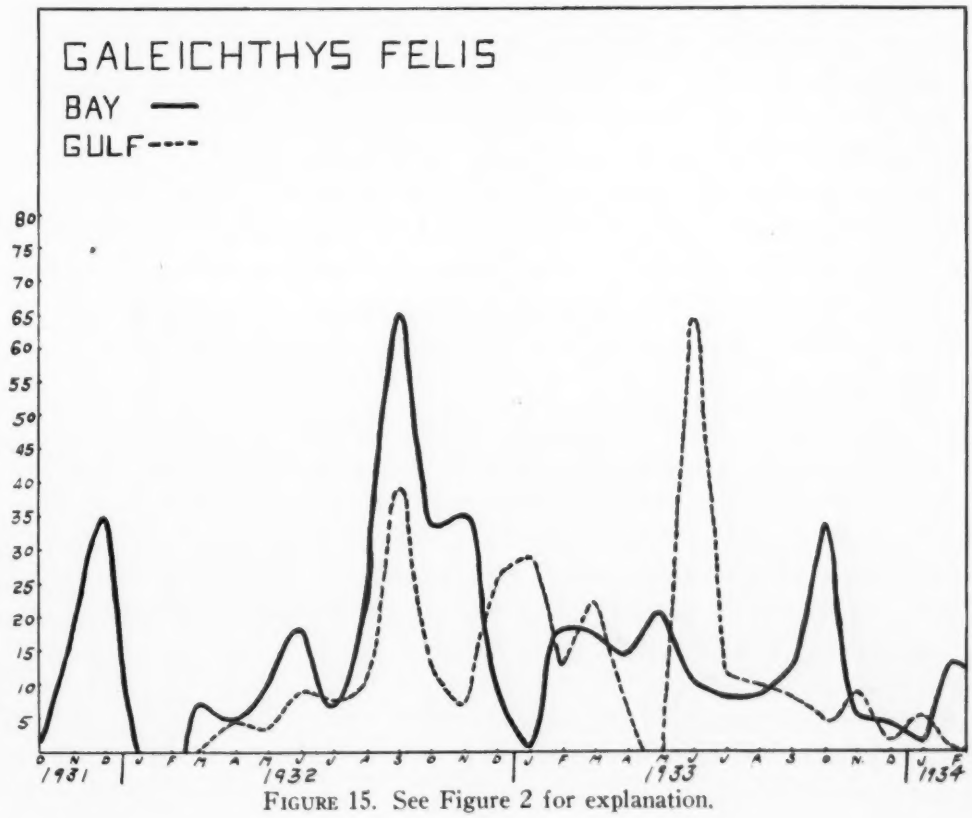

FIGURE 15. See Figure 2 for explanation.

December, 1932, to May, 1933, in the bay. It was caught on the outside in February and March, 1934. It is clear that this fish appears inshore only during the cooler months of the year. It is interesting to note that the winter of 1931-32 was exceptionally mild, except for one cold spell in the month of March during which freezing temperatures extended to the coast. *Urophycis floridanus* appeared after the cold spell. Jordan and Evermann (1898) noted the winter appearance of this species around Pensacola. Hildebrand and Schroeder (1928) noted the same thing for *U. chuss* in Chesapeake Bay. *U. floridanus* is a deep water species. It was present in Barataria Bay in winter and early spring when the salinities were very low. Although it is a salt water denizen it seems to be tolerant of low salinity and is probably kept out of the bay in summer by the higher temperatures in shallow waters.

HETEROSOMATA

Of the seven species of this order caught, namely, *Trinectes maculatus, Achirus lineatus, Citharichthys spilopterus, Etropus crossotus, Symphurus plagiusa, Paralichthys lethostigmus,* and *Ancylopsetta quadrocellatus,* the curves for all except the last two and *Achirus lineatus* have a very outstanding peak in September, 1932. The last two fishes were caught too rarely for any conclusion to be drawn about them, and *Achirus lineatus* had the peak in October rather than September. The next year the mode fell in October and was so slight for some as to be scarcely noticed. In 1934 there was also a mode for March on the outside, common to the same species except for *A. lineatus.* It is probable that this last mode was caused by spawning animals.

Whatever the affinity or relationship which causes the close resemblance in this phase of the life history of these flatfish it must be quite strong for it embraces five species in three different families. The number of species and the similarity of the curves for three years and at different times of the year make it impossible for the phenomenon to be a matter of chance. The curves for each species being so similar, they were combined and presented in Figure 16.

Citharichthys spilopterus (Günther)

This species was caught very little in the gulf. In the bay it was not plentiful and in some months was not caught. In September, 1932, and October, 1933, the abundance peak was marked as was the case with close relatives of the fish. This was not caused by young individuals. Possibly it was caused by the migration of adult and half-grown fish from shallow to deeper water before the approach of winter.

Etropus crossotus (Jordan and Gilbert)

The abundance variation of this species is practically the same as that for *Citharichthys spilopterus,* with the difference that there was a peak on the

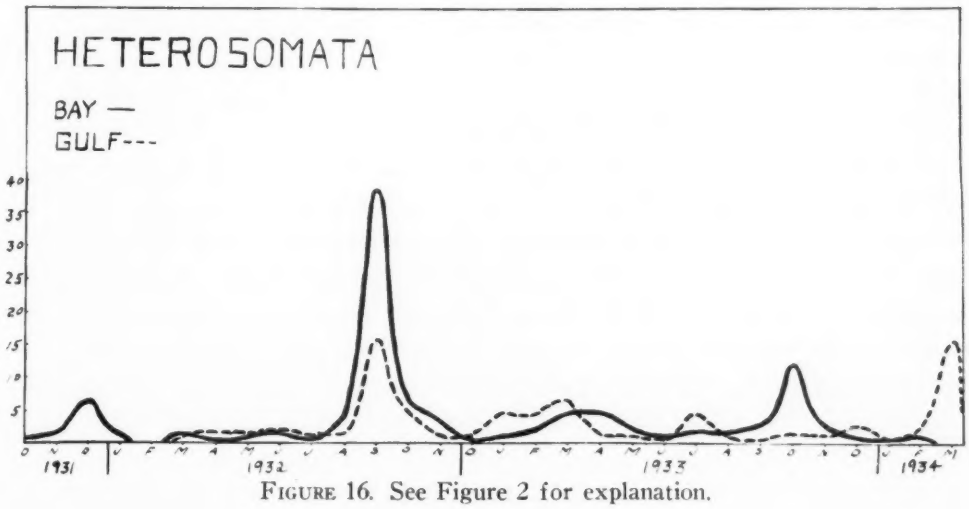

FIGURE 16. See Figure 2 for explanation.

outside corresponding to that on the inside in September, 1932. It was numerous on the outside in July, 1933; just why is not known, and no such increase was noted in any other year.

Paralichthys lethostigmus (Jordan and Gilbert)

Rarely this fish was taken in the gulf. In the bay it was never plentiful in trawl catches. In April, 1933, numerous small fish from 5 to 10 cm. in length were taken on outside beaches in seines. From a month to two months later this species appeared in trawl catches at a size of 12 to 15 cm. in length. Hildebrand and Cable (1930) give evidence to show that *Paralichthys dentatus* spawns from September to April at Beaufort, N. C. Using the size of the young as a criterion it seems that the spawning of *Paralichthys lethostigmus* in Louisiana corresponds somewhat to that time, and the young grow amply large enough to be taken in the trawls the following year.

Achirus lineatus (Linnaeus)

This sole was not common either in the gulf or the bay. It was most numerous from September to November in 1932 with the highest point in October on the inside. There was no pronounced increase in the gulf. The following year the fish were most common in October.

Trinectes maculatus (Bloch and Schneider)

Like other members of the order *Heterosomata* there was a great abundance of the hogchoker in September, 1932, both in Barataria Bay and the Gulf of Mexico. In 1933 the peak was in October and for the inside only. There was a movement of fish from the gulf back into the bay in the spring in 1933. At this time a number of small fish were caught, which had evidently hatched the previous year, along with fish with well-developed ovaries, which were present in April, May and June, 1933. The spring catch was made up

of these two size groups. Hildebrand and Schroeder (1928) noted ripe fish in June, July and August in Chesapeake Bay.

Symphurus plagiusa (Linnaeus)

The appearance of the tonguefish was more or less sporadic both inside and outside. In both localities there was a marked abundance in September, 1932. In 1933 there was a slight increase in October for the bay only. In March, 1934, there was a peak in the gulf as there was for other species of the order. This fish is necessarily a slow swimmer and is therefore scarcely given to extensive migration from place to place. The sudden changes in abundance (Tables 1 and 2) must then be due to migrations to and from shallow water close to shore and the open bay or gulf. Small planktonic, symmetrical animals were taken in April, 1933, in the gulf. According to Hildebrand and Cable (1930) small fry of *Symphurus plagiusa* were present at Beaufort from May to October.

DASYATIDAE

Dasyatis sabina (Le Sueur)

The stingaree was seldom caught in the gulf (Table 2). In the bay it was caught more or less throughout the year. On February 4, 1933, seven males with milt were taken in one haul at the head of the bay. On February 16 another male in like condition was caught. On June 5, 1932, the writer observed a large female in moribund condition give birth to three young, one of which swam away after being placed in the water. These observations indicate that the approximate length of time the developing egg is held in the female is three or four months. Some writers say that this ray breeds all the year around, but no indication of this was seen.

DISCUSSION

The data presented are chiefly descriptive and are more valuable in this aspect than for purposes of analyses. Many unanswered questions have arisen, but the knowledge of these is an advance and some may be used as the starting point for future work.

For many species studied, namely, *Trinectes maculatus, Achirus lineatus, Citharichthys spilopterus, Etropus crossotus, Symphurus plagiusa, Cynoscion nebulosus, Brevoortia patronus, Galeichthys felis, Bagre marinus, Leiostomus xanthurus* and *Bairdiella chrysura,* there was a recurrent, sequential phase in the life history or annual cycle of the fish, when there was a sharp abundance mode. These fell at certain times of the year and can be expected to recur at about the same time in future years. Fishes of this group are differentiated arbitrarily from those such as *Micropogon undulatus* which has a wider period of increased numbers. *Polynemus octonemus* and *Vomer setapinnis*

came and went at certain times of the year, so that their arrivals and departures might be predicted with some accuracy.

The place or worth of observations on seasonal variations in abundance may be brought out by the words of Stuart Mill (1848), who said: "Of all truths relating to phenomena, the most valuable to us are those which relate to their order of succession. On a knowledge of these is founded every reasonable anticipation of future facts, and whatever power we possess of influencing these facts to our advantage." An example will illustrate. A study of the year groups of a fish might well be made at the time of its greatest numbers. If the abundance is due to the young, as was found here in many instances, studies of the numerical ratio of the zero year group to other groups, at the time of the peak, might be of aid in predicting the future abundance of year classes.

The time of greatest numbers in the annual cycle of a fish is that immediately following the hatching of the eggs. Thereafter there is a sharp decline due to the heavy mortality of the young, and the decline continues until the next reproductive period, although due to rapid individual growth the actual species mass may increase during part of this period. Yet the so-called peaks or abundance modes may be noted at a later date and may appear at different times for the different devices used for capture of the fish. In other words the peaks are to a certain extent dependent on the type of gear used, whether it be otter trawl, beam trawl, seine, plankton net or something else. Plankton nets will capture larval fish, but will fail to take larger specimens which may cause a peak of numbers in trawl hauls at a later date. A simple corollary of this fact is that the same collecting gear should be used from year to year in studying seasonal variations in the numbers of fishes.

In the study of variations in animal numbers from year to year or comparative abundance of species to species (Elton, 1927) it is of prime importance to recognize that there is an annual cycle of change in numbers taking place during the year and to know when it is taking place. An enumeration of animals at one time of the year would have to be compared to counts of other years at the same seasons. Several counts at different seasons of the year, compared to like counts in other years, would be much more valuable.

It is quite evident that the bay waters act as nursery grounds for many of the species studied here. The smaller fishes were practically always found inside, while larger individuals were taken in the gulf. Pearson (1929) has presented data to show that most of the *Sciaenidae* spawn in the gulf, and observations indicate that most fish discussed here did the same. Some of the evidence is indirect such as that for *Polynemus octonemus* and *Leiostomus xanthurus,* the small individuals of these species being taken in plankton tows in the gulf before being caught in the bay. Exceptions to this rule are *Galeichthys felis, Bagre marinus* and *Dasyatis sabina,* for which data have been presented, and probably *Cynoscion nebulosus.*

Certain fishes were found to frequent the bay waters, while others preferred the open gulf. This has been discussed under each species. More data on this point were given by Gunter (1938). It was noted that young individuals of many species preferred or possibly were able to stand low temperatures and salinities of the bay during winter better than older fishes.

It has been shown (Gunter, 1936) that from late spring to early fall is the time of greatest catches of fish in trawls and that the catches in the gulf become larger in the late summer. This apparently is due to the migration of young fish from the bay to the gulf as they grow up.

A very clear seasonal cycle and seasonal biological succession was observed in this region. There is a period of low temperatures during the winter in the bay. In the winter and spring the salinities are quite low. At this time the water at the upper part of the bay is practically fresh. The condition extends somewhat to the outside. On two consecutive years in the late winter and early spring, *Cynoscion nebulosus* was taken in the gulf. The alligator gar was also taken in the gulf during these months. At the same time the fresh-water catfish, *Ictalurus furcatus,* and the river shrimp, *Macrobrachium ohionis,* appeared in the bay. The migration of the latter animal into brackish water has been recorded before by Gunter (1937). These animals are probably more influenced by salinity than temperature. On the other hand *Urophycis floridanus* came from deep water to the bay in winter and the only appearance of *Cynoscion nothus* in the bay was noted in the months of December, January and May. With these two fishes temperature and not salinity was probably the governing factor. Galtsoff (1924) says that mackerel in the Black Sea are very sensitive to temperature, but not to salinity. Ekman (Petterson, 1912) has shown that herring are very sensitive to slight variations in salinity.

During the winter sharks, jackfish and many of the *Carangidae* absented themselves from the bay as well as from that part of the gulf explored by the trawls. In the summer as *Urophycis floridanus,* the fresh-water catfish, and the river shrimp retreat to their respective abodes, the sharks, jacks, threadfins and others return to the shore waters of the gulf. As the summer progresses and the temperatures and salinity of the bay rise some of these fishes move into it and remain there until autumn and the return of low temperatures, whereupon they move back into the gulf and later depart for deep water as the river shrimp, fresh-water cat, and *Urophycis floridanus* return, thus completing a cycle.

SUMMARY

The data for this paper are monthly abundance variations of fishes in trawl catches on the Louisiana coast in Barataria Bay and the Gulf of Mexico, supplemented by general observations and a small number of total length measurements. The time of observation was two and one half years.

There was a sequential, seasonal, yearly variation in numbers of the larger part of the species studied. Knowledge of these variations helps elucidate the life histories of fishes about which something is known, such as the Otolithidae and some Sciaenidae, and gives new light on many hitherto unstudied species, which, however, is fragmentary in some instances.

The data were separated for bay and gulf waters so that movements of the population from one locality to the other could be pictured in some instances. Fishes taken in the bay were smaller than those taken in the gulf. The bay serves as nursery grounds for most of the species studied, although most of them seem to spawn in the open gulf. The young fishes gradually move to the outside as they grow up.

Some fishes are only seasonal residents in the area and the time of their arrivals and departures were rather definite.

A seasonal biological succession of the fish population is briefly described and discussed.

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ECOLOGICAL STUDIES ON THE VERTEBRATE FAUNA OF A 500-ACRE FARM IN KALAMAZOO COUNTY, MICHIGAN

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ECOLOGICAL STUDIES ON THE VERTEBRATE FAUNA OF A 500-ACRE FARM IN KALAMAZOO COUNTY, MICHIGAN

INTRODUCTION

Quantitative research on animal populations has to a considerable extent been restricted to small areas and small animals. Among the best known works of this nature are those of McAtee (1907), Beebe (1916), Wolcott (1918, 1937), Sanders and Shelford (1922), Weese (1924), Blake (1925), Smith (1928), Shackleford (1929), and Townsend (1935). Small controllable populations of invertebrates have served to reveal fundamental principles of population dynamics (Chapman 1928) that may, perhaps, be applicable to all forms; but specific information as to the actual numbers and relationships of vertebrate animals on representative areas is almost wanting.

The study most nearly comparable to what is attempted here is that of Williams (1936), who made a quantitative analysis of a unit of beech-maple forest. The author also investigated the interrelationships of the constituents involved, and discusses the dynamics of the community. Apparently this is the first detailed area study that includes quantitative work on the larger vertebrates.

It is not difficult to account for the small number of investigations that have been made in this field. There are numerous significant obstacles to area studies involving the handling of large populations of birds and mammals. Continuous year-round field work is very desirable if the annual population cycles are to be interpreted, and this is seldom possible. Territory suitable for such work should, for maximum significance, be fairly representative of widespread conditions. It must also be under control as to policies regarding the trapping, shooting, and management of its animal populations. Such areas are not plentiful. In addition to these considerations, the equipment and help necessary for continuous work on a large number of species have not often been available to the student.

The present study results from a cooperative effort on the part of Michigan State College and the Michigan Department of Conservation. Preliminary work was done during the fall, spring, and summer of 1934-35 under a graduate assistantship in zoology at the W. K. Kellogg Bird Sanctuary. From September, 1935 to August, 1937 the study was supported by a half-time research fellowship provided by the Game Division, Department of Conservation. Equipment and expenses also were furnished. Although the interests of the Department of Conservation in these animal populations have principally to do with their value for sport and fur, I have not been limited to a study of game birds and mammals. It has been fully realized that the community of animals associated here must be demonstrated in its entirety before the position of individual species can be appreciated.

Gratitude is here expressed to the Michigan Department of Conservation and in particular to Mr. H. D. Ruhl, in charge of the Game Division, for providing a two-year fellowship and other means of pursuing these studies. Grateful acknowledgement for guidance is made to Dr. M. D. Pirnie, Director of the W. K. Kellogg Bird Sanctuary and chairman of the graduate committee; to Dr. H. T. Darlington of the Botany Department of Michigan State College, who gave needed instruction and criticism in the botanical studies; to Dr. H. R. Hunt, Head, Mr. J. W. Stack, and Mr. Burton T. Ostenson of the Department of Zoology, and to Dean E. A. Bessey of the Graduate School of Michigan State College.

For helpful suggestions and assistance in field work I am indebted to Mr. Farley F. Tubbs, Mr. Paul Hickie, and Dr. G. W. Bradt of the Game Division, Michigan Department of Conservation. Mr. C. M. McCrary, Superintendent of the W. K. Kellogg Farm, cooperated in matters of policy and contributed numerous field observations. Mr. Homer Bradley and Dr. Carl Gower of the W. K. Kellogg Bird Sanctuary gave many valuable field records. This investigation benefited greatly from the services of Mr. Curtis Bartlett who for two winters was transferred from the State Game Farm to assist in the study.

The area upon which the work was done is owned and operated by Michigan State College. Under these circumstances policies have been under reasonable control. Residence at the Kellogg Bird Sanctuary from April, 1935 until August, 1937 has permitted a continuous study. All of my own time was devoted to the work after September, 1935, and a full-time assistant was on the project from October to April during both years.

In scope this study is limited principally to upland forms. Thus no particular investigation has been made of the muskrat, and waterfowl are treated only incidentally. The work has been featured mainly by two activities: the intensive use of box traps during the winter months, and daily field work throughout the year. Both of these methods have been of great value in obtaining the data presented.

The object of this paper is threefold: (1) The area will be analyzed in terms of its physical characteristics and plant habitats. This is necessary to a proper evaluation of the data on animal populations. (2) There is presented a quantitative study of the resident birds and mammals with special reference to the larger species of greater abundance. Where actual population figures are not available the relative numbers of different animals are indicated. (3) The last portion of the work is devoted to a discussion of the interrelationships of these animals with reference to the use of habitats, seasonal and daily times of activity, and to the position of each in the food cycle. In the appendix is given a complete check-list, with scientific names, of all vertebrate species recorded on the area during this work. Hence, for the sake of brevity, vernacular names are usually used in the text.

This is an area study. A unit of the earth's surface, occupied and modified by man, is being described in terms of its plant covering and the animal forms that have found it possible to live here.

THE AREA STUDIED

The territory included in this study is 500 acres in extent and is located in Section 8, Ross Township, Kalamazoo County, Michigan. It includes Wintergreen Lake, which is about 20 acres in area. The southwest corner of Section 8 lies in Gull Lake, the largest body of water in this portion of the state. Along the shore of the lake and separated from the Kellogg Farm by a road is Midland Park. This resort is a collection of cottages, all of which are occupied in summer and where a few people remain in winter. It lies on the flats next to the lake amid a grove of second-growth oaks. On the west the farm is adjacent to two private Gull Lake estates. On the north, east, and south it is bounded by similar farm land.

PHYSIOGRAPHY AND SOILS

The locality treated lies on an extensive outwash plain which was formed in the angle of the Lake Michigan and Saginaw lobes when the ice border was only a few miles from the present site of Gull Lake (Scott, 1921). The region is characterized by pit lakes and kettle holes which, presumably, were formed by the burying of ice blocks which melted and left basins sunk below the surface of the plain. Wintergreen and Gull lakes were probably so formed, as were the five small kettle holes found on the farm.

Wintergreen Lake lies at the 891-foot contour. The highest point on the area is southeast of the sanctuary and is 935 feet above sea level. The sanctuary and that portion of the farm to the west and east are too hilly for cultivation. The level parts of the farm are on the east and north borders. It is in these fields that the cultivated crops are raised.

The soil of the Kellogg Farm is a Bellefontaine sandy loam (Perkins and Tyson, 1926). It is variable as to humus content and in spots is quite sandy. According to the classification of Veatch (1933) it varies locally from first- to third-class farmland. Where the fields are level excellent crops of grain and hay are raised in good seasons. Leverett (1917) gives the principal crops of Kalamazoo County as hay, corn, wheat, oats, potatoes, and rye, and the average value per acre (1917) as $41.72. Perkins and Tyson give the value of Bellefontaine sandy loam as from $30 to $150 per acre, according to location and improvements.

CLIMATE

Kalamazoo County has an average growing season of from 150 to 160 days (Schneider, 1917). The average date of the last killing frost is May 1 to 5. The first killing frost occurs after October 10. Annual precipitation in this portion of the county is usually between 30 and 34 inches (Hill, Riddle, and Elliott, 1930). The mean annual temperature at Kalamazoo is 47.9° F. (Perkins and Tyson, 1926). The summer and winter means are 69.9° F. and 24.9° F., respectively. This project benefited greatly from the presence of a United States Weather Bureau Station (the Gull Lake Station) at the Kellogg Farm. Thus complete weather data were kept on the exact location of the study.

The two seasons of the work were extremely dissimilar. The 1935 growing season was very favorable to all plant life. As a consequence, herbaceous cover was high in the fall and an excellent crop of wild fruits and seeds was produced. The ensuing winter was one of low temperatures and heavy snows which, late in February, reached a depth of 26 inches. Due to the protecting snow very little ice formed on the swales, and soil on the uplands was frozen to a depth of only a few inches.

The summer of 1936 was one of extreme drouth. A new high temperature (108° F.) was recorded for the Gull Lake Station.[1] Crops were much curtailed throughout the region, and fall cover was not so heavy as in the preceding season. The winter that followed was as mild as the winter of 1935-36 had been severe. The ground was bare much of the time, and although temperatures were comparatively high during most of the season, the soil froze to an average depth of nearly a foot.

As the two growing seasons and their effects are important for the purposes of this work, the compiled weather data are for the 2-year period from April 1, 1935 to April 1, 1937. Figure 1 is a climograph comparing mean monthly temperatures and precipitation for the two years beginning April, 1935 and April, 1936. The extent to which the two years differed is readily apparent. Other weather data will be adduced as they are necessary to particular phases of the work.

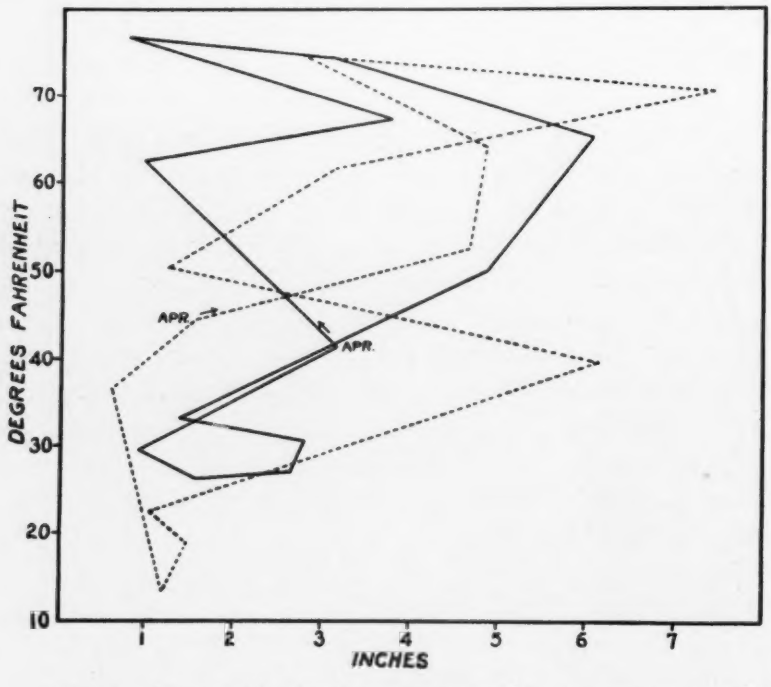

FIG. 1. Climograph showing mean monthly temperatures and precipitation for the two years beginning April, 1935 (dotted line) and April, 1936 (solid line).

[1] Established April, 1929.

RECENT HISTORY

Several farms which then composed this area were purchased by Mr. W. K. Kellogg in 1927, and a year later the entire tract was given to Michigan State College. Eighty acres around Wintergreen Lake were fenced off as the W. K. Kellogg Bird Sanctuary, while the surrounding land became the W. K. Kellogg Farm. The Bird Sanctuary is primarily a waterfowl refuge. In November, at the height of the migration, 3000 ducks of from 10 to 15 species and 500 Canada geese may at one time be found using the lake. From 100 to 300 geese usually remain in the vicinity and feed on the fields in early winter. In the spring it is common for 20 or 30 pairs of mallards and from 10 to 15 pairs of geese to nest around the lake and swales. In summer and winter only a few hundred waterfowl (some captive) occupy the lake and apparently do not greatly affect the resident upland species of the area. The Farm is operated by the college for experimental and demonstration purposes. Corn, wheat, oats, and alfalfa hay are raised; a dairy herd and sheep are kept; and a large poultry plant is operated. In this study no distinction has been made between the territory of the sanctuary and of the farm. Except where the sanctuary is specifically designated, the entire 500 acres is referred to as the Kellogg Farm.

During 1927 extensive plantations of conifers, aggregating about 5000 trees, were set out on the sanctuary and the portions of the farm adjoining to the east and west (fig. 2). Since that time also the natural deciduous brush around the swale and lake margins, which was formerly held back by

FIG. 2. Coniferous plantations on the W. K. Kellogg Bird Sanctuary in the winter of 1935-36.

grazing, has been allowed to increase into dense coverts (fig. 3). Washes that had started on steep slopes have been filled with stumps. The area apparently supports much more cover now than it did before the sanctuary was established. Otherwise it does not greatly differ from other farm land in the region. Figure 4 shows the distribution of the principal winter cover types during this study.

At the sanctuary the regular winter feeding of small grains has supplemented the natural foods of pheasants and quail. In the winters of 1933 and 1934 standing corn was left in a field at the approximate center of the farm. Chicken house litter containing cracked corn was spread on some fields at two-week intervals through most of every winter. This also has added to the food supply of ground-feeding birds. During this study a few feeding stations were operated for experimental purposes during the winter of 1935-36, and several rye patches also provided food that was available until spring. During the following winter no feeding was done.

The farm area has not been open to general hunting since 1927. The land around Gull Lake for a quarter of a mile back from the shore was closed by an act of the legislature in 1927 and became a sanctuary for all species except rabbits. From 1927 until 1930 intensive "predator control" was practiced at the sanctuary. Steel traps and box traps were constantly set, and all carnivorous mammals and birds were killed as fast as they could be caught. From 1931 to 1935 a small number of skunks, weasels, opossums, hawks, and great horned owls were taken; but the program was not carried on with anything like its former intensity. During this investigation rabbits have been the only

FIG. 3. The west shoreline of Wintergreen Lake showing the dense deciduous brush that has sprung up here since 1927.

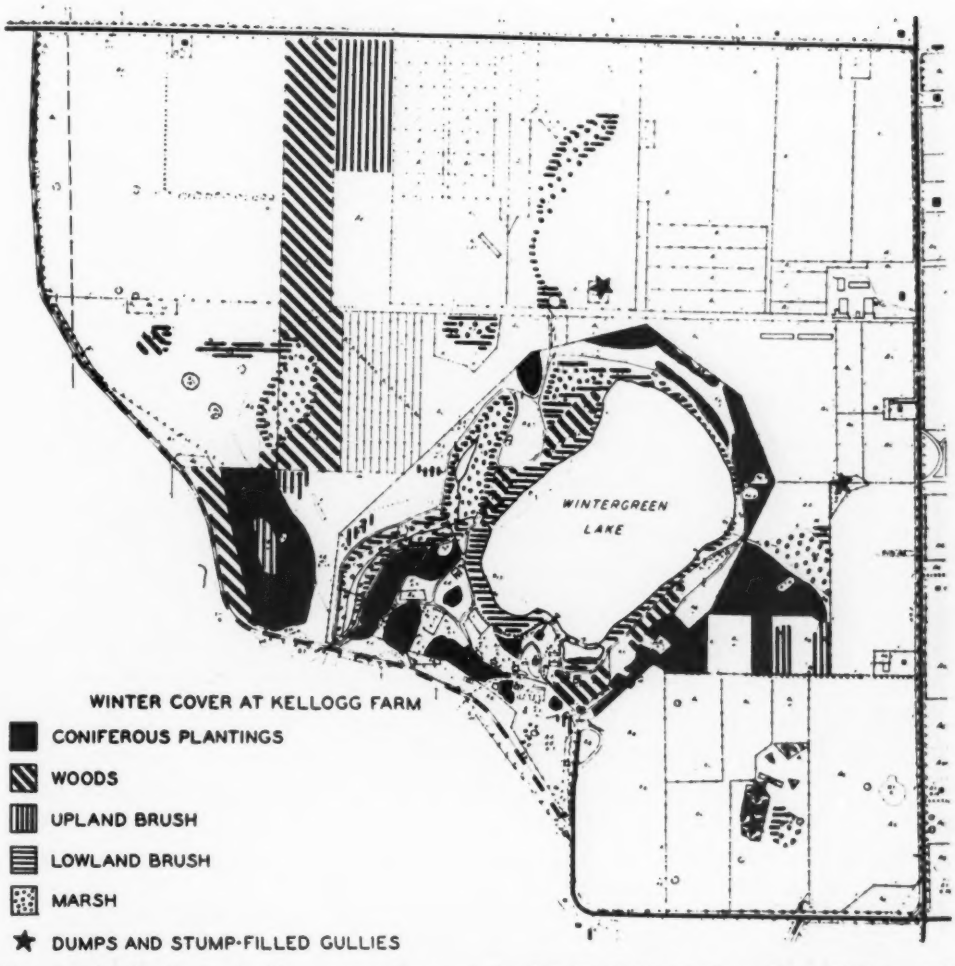

FIG. 4. Distribution of winter cover types on the W. K. Kellogg Farm from 1935 to 1937.

species killed on the area until the population studies were completed in the winter of 1937.

VEGETATION

The Region in General

This portion of Michigan was originally covered by a subclimax forest of oak and hickory. That this is a seral stage dependent upon edaphic conditions is shown by the occupation of the richer and more mesophytic soils by beech and maple, which may be considered the true climax for this region, and which may be expected gradually to replace the more xerophytic oak-hickory stage. As the region has been recently glaciated, the topography is still young. A great variety of conditions exists between the hydrophytic lakes on the one hand and the xerophytic hills on the other. As the hills are eroded and the lakes are filled the mesophytic areas increase (Cowles, 1901) and may, under natural conditions, be expected eventually to characterize the region.

The nature of the original forest was described by Durant (1880) and by Thomas who, writing in 1869 says, "—the surface is rolling—and is composed principally of oak openings with some beech and maple skirting the river and some of the creeks."[2] As the Kellogg Farm supports no beech-maple the entire area may be considered developmental from the standpoint of succession. The hydrosere[3] is represented in the kettle holes and Wintergreen Lake, while the stages of the xerosere may be found on the upland. As the latter are artificial in origin (due to the activities of man) they are classed here as belonging to a secondary succession in contradistinction to the natural, or primary, hydrosere (Weaver and Clements, 1929). The sere is used as a convenient vehicle for the presentation of habitat data. The natural, or prisere, is given first, with later a discussion of the main type of secondary succession found here (succession from plowed ground). The artificial plantings are treated under the heading "Artificial cover types."

Habitat Types on Kellogg Farm

In this work the term "predominant" has been used to indicate animals active throughout the year. From the same standpoint all others are "seasonals" (Smith, 1928). In designating an animal species as "characteristic" of a given habitat it is implied that the species has shown a marked predilection for that type of environment. Species may not be listed as characteristic of any habitat on the area either because observations are too few to justify it, or because the animal has made extensive use of several habitats. Thus such important animals as the cottontail rabbit, skunk, and pheasant cannot be said to belong to any particular habitat, considering their behavior during the entire year.

Primary Succession, a Hydrosere

Open Water Habitat.—This habitat is present only in Wintergreen Lake. It is not treated in this study and is mentioned only as the initial stage in the hydrosere. A list of the fishes and amphibia found in the lake is given in the appendix (see check-list of vertebrates for the area, p. 430).

Marsh Habitat.—The total area of this habitat is approximately ten acres. It is divided into six principal units, the largest of which is the long swale along the outlet of Wintergreen Lake on the sanctuary. Although the water level here is variable, it does not normally fluctuate to the extent that it does in undrained marshes. The level of the lake itself must drop several feet before these swales become dry. The undrained kettle holes on the area (four in number) are, typically, small units of marsh surrounded by a narrow belt of swale brush. These two habitats are clearly defined and hence are discussed separately. Swales are much influenced by the amount of rainfall in any par-

[2] Kalamazoo River.

[3] The parts of this area that are now covered by oak woods have, since the advent of man, never supported any other type of cover. Hence these areas may be said to have developed by natural stages with no artificial interference. This type of natural sere is designated a primary succession or prisere. The lowest stage of this natural succession is open water; hence it is a hydrosere. The alternative condition is succession starting from bare soil or rock. In such a case the unit succession is termed a xerosere. All the stages of a natural xerosere do not occur on this area.

ticular season. During an exceptionally dry year the buttonbush of the brushy margins actively invades the marsh. A correspondingly wet year retards this invasion.

The marsh habitat varies considerably with the season and with the extent to which the deposition of humus in any particular swale has tended to fill it in and to render the area more xeric.

In the deepest parts of the swales the water is several feet in depth and the bottom is soft partially-decayed humus. Here the most characteristic hydrophyte is *Nymphozanthus advenus* (yellow pond lily). *Polygonum coccineum* (water smartweed) is often found in pure growths, particularly along edges where the rhizomes extend beneath the soil and connect with sprouts on the bank. In May of 1935 the water of the swales was in many places completely covered with the small thalli of the floating liverwort *Ricciocarpos natans*. In this season duckweeds were very scarce. In the 1936 season little Ricciocarpos was present, but the duckweeds *Spirodela polyrhiza* and *Lemna minor* occurred in small quantities. Waterfowl fed upon all these natant plants.

In shallow parts of the water a solid stand of *Typha latifolia* (cat-tail) sometimes occurs to the exclusion of all other species. This plant is found more sparingly in the swales that become dry in late summer. Here *Carex* sp. (sedge), *Phalaris arundinacea* (reed canary grass), *Calamagrostis canadensis* (blue-joint grass), and *Polygonum sagittatum* (arrow-leaved tear-thumb) are more common. In one swale *Eleocharis palustris* (spike rush) occurs. Other common plants of this habitat are *Asclepias incarnata* (swamp milkweed), *Rumex verticillatus* (swamp dock), and in shaded places *Impatiens biflora* (jewel weed).

A small swale on the east side of the farm has been drained by a ditch leading into the lake. There is no standing water here at any season and conditions are dryer than in the other marsh areas. A very few square feet of moist ground at the center are occupied by *Polygonum hydropiper* (water pepper) and around it an extensive solid growth of *Polygonum sagittatum* extends out to the edges of the former marsh. We find a similar condition in the dryer portions of other kettle holes. The above plants, as well as *Polygonum persicaria* (lady's thumb), *Polygonum pennsylvanicum* (Pennsylvania smartweed), *Polygonum orientale* (prince's feather), and *Polygonum acre* (smartweed) are to be found around the lake and the various swales where moisture conditions are favorable. Many of these species produce winter foods of value to seed-eating birds.

The following animals may be considered characteristic of the marsh habitat on this area:

Amphibians

Pseudacris triseriata (Swamp tree frog)
Hyla crucifer (Spring peeper)
Rana pipiens (Leopard frog)

Reptiles

Emys blandingii (Blanding turtle)

Birds

Agelius p. phoenicus (Redwing blackbird)

Botaurus lentiginosus (American bittern)

Porzana carolina (Sora rail)

Anas p. platyrhynchos (Mallard duck)

Mammals

Ondatra z. zibethica (Muskrat).

All of these amphibians are inactive in winter. The birds also are absent at this season. The muskrat alone is active throughout the year and thus is the only predominant animal of this habitat.

Lowland Brush Habitat.—The irregularity of this habitat and the fact that it occurs in small units render its total area difficult to compute. It is probably near eight acres. Its spotty distribution and the fact that it often is present in long narrow strips make it of more importance to animal species than would be inferred from its actual area. This habitat borders most of the shore line of the lake and forms a brushy margin around the greater portion of the swales.

The lowland brush habitat may be divided into three principal types. *Cephalanthus occidentalis* (buttonbush) is a well-defined type which exists in comparatively pure stands in the wetter portions of the habitat. Exceptionally wet weather retards its invasion of the water but does not kill it out. In dry years it makes rapid progress.

A second type of swale brush, usually found outside (away from the water) and on dryer soil than the buttonbush, is characterized by a mixture of *Cornus candidissima* (gray dogwood), *Cornus amomum* (silky dogwood), *Cornus stolonifera* (red-osier dogwood), *Sambucus canadensis* (black elder), and various less plentiful shrubs such as *Rosa* sp. (bush rose), *Viburnum lentago* (nannyberry), *Amelanchier canadensis* (service berry), and others. The mixed shrubs constitute the most exensive swale brush type. It is variable, often with one of the constituents, such as gray dogwood, red-osier dogwood, or elder, forming a pure stand locally.

A third distinct type of lowland brush is willow. In spots of low sandy soil that are not too wet *Salix longifolia* (sandbar willow) flourishes. The stems are typically from eight to ten feet in height and grow in close, pure stands. The best example of this growth is in the large kettle hole on the west side of the farm. In much the same type of situation an active growth of *Populus tremuloides* (quaking aspen) is sometimes found. The young shoots are often mixed with the shrubs, and in dryer places the larger trees may assume dominance.

There are numerous other plants that are typically associated with the above brusy types. *Salix bebbiana* (Bebb willow), *Salix petiolaris,* and *Salix*

FIG. 5. An undrained kettle hole on the Kellogg Farm showing willow brush in the foreground, an extensive growth of reed canary grass in the marsh, and the upland woods in the background.

FIG. 6. The appearance in winter of the same kettle hole shown in fig. 5.

discolor (pussy willow) are common as shrubs, while *Salix nigra* (black willow) and *Salix amygdaloides* (peach-leaved willow) become large trees and occur as individuals here and there along the swale and lake margins. In openings among the larger shrubs *Spiraea alba* (meadow sweet), *Rubus idaeus strigosus* (red raspberry) and such herbaceous forms as *Urtica gracilis* (nettle), *Thelypteris palustris* (swamp fern), and *Phytolacca americana* (pokeberry) are common. *Cuscuta pentagona* (dodder) and *Polygonum scandens* (climbing false buckwheat) are often found vining through the marsh plants or over the buttonbush respectively.

This habitat forms the most important natural winter cover on the area. Although many animals live in it, few are restricted to it. The greatest discrimination in favor of the swale brush is shown by certain species of nesting birds.

Birds

Dendroica a. aestiva (Yellow warbler)
Empidonax t. trailli (Alder flycatcher)
Dumtella carolinensis (Catbird)
Melospiza m. melodia (Eastern song sparrow)

Mammals

Zapus h. hudsonius (Meadow jumping mouse)
Peromyscus leucopus noveboracensis (Northern white-footed mouse)
Blarina b. brevicauda (Short-tailed shrew)

Of the above animals the white-footed mouse and the short-tailed shrew are predominants.

Lowland Woods Habitat.—Lowland woods is the least extensive of the major habitats found on the Kellogg Farm. It is present only as a trace that tends to mix with the upland woods on low ground. Around the large kettle hole at the south end of the farm woods is the best-defined unit. It is probably less than an acre in extent, although mixture with the upland type makes difficult the setting of limits. North of the outlet of Wintergreen Lake, between the lake and the swale, the presence of considerable red maple gives the growth a low woods character, although the upland oaks are numerous here also.

The most definitive species of this habitat are *Acer rubrum* (red maple), *Ulmus americana* (American elm), and *Fraxinus americana* (white ash). Associated with these trees *Laportea canadensis* (wood nettle), *Impatiens biflora* (jewel weed), and *Parthenocissus quinquefolia* (Virginia creeper) are common. Due to its limited extent no vertebrate animals in particular can be said to characterize the habitat on this area.

Upland Woods Habitat.—On the farm and sanctuary there are approximately 30 acres of oak woodland, which is divided into four principal areas. The largest of these is in the northwest quarter of the farm and is a little under 20 acres in extent. Another plot of woodland lies on the southwest

boundary. The latter is all second growth, having been completely cut off within recent times. Only about two acres of this is within the area studied. The trees are from six to ten inches in diameter, and there is a considerable admixture of *Populus grandidentata* (large-tooth aspen). This species, as would be expected, is fast giving way to the oaks. The oldest oak areas are on the sanctuary. To the southeast of Wintergreen Lake the growth lies in a divided strip of less than three acres. On the northwest side of the lake the "sanctuary woods" forms a unit of about two acres. Cutting has not been extensive in these areas and many of the trees (18 to 24 inches in diameter) may be considered a part of the original forest.

As before stated the upland oak woods represents the most advanced seral stage present on this area. The largest woodlot of twenty acres functions most characteristically on account of its size and is referred to in this description.

The trees most typical of the habitat are oak and hickory. Of the three species of oak present *Quercus velutina* (black oak) is the most abundant, with *Quercus borealis maxima* (red oak) second in importance. *Quercus alba* (white oak) is the least common of the three. Among the oaks is to be found a fairly constant mixture of *Carya glabra* (pignut hickory), *Prunus serotina* (wild black cherry), *Acer rubrum* (red maple), and, in spots, *Fraxinus americana* (white ash). Red maple and ash are more characteristic of the low woodland habitat but often occur as secondary species in the upland oak woods of this region, becoming more numerous in locations of greater moisture.

A few of the oaks are from 18 to 24 inches in diameter. These probably were young trees when the first cutting was done in this locality. Stumps in varying stages of decay show that selective cutting has very probably been going on for fifty years or more. Around the larger and older stumps will sometimes be found a stand of young oaks nearly uniform in size. All the dead, hollow, and misshapen trees have been removed recently for firewood. Few ground logs are present and these are small.

The woods is naturally open in character and in spots a few individuals of *Cornus florida* (flowering dogwood) or *Malus coronaria* (wild crab) occur, with here and there a fairly dense growth of *Sassafras officinale* (sassafras). In areas of increased insolation a sparse tangle of *Rubus allegheniensis* (blackberry) and *Rubus idaeus strigosus* (red raspberry) is produced. Individuals of *Ribes floridum* (wild black currant), *Ribes cynosbati* (wild gooseberry) and a bush rose, *Rosa* sp., are to be found at intervals in the stand.

Throughout most of this habitat there occurs a sparse growth of *Poa pratensis* (Kentucky bluegrass), *Poa compressa* (Canada bluegrass), or a fine grass-like sedge, *Carex* sp. A moss, *Polytrichum* sp., is common in the more shaded portions.

Among the characteristic herbs of the woods floor are *Claytonia virginica* (spring beauty), *Hepatica americana* (hepatica), *Viola cucullata* (blue violet), *Erythronium albidum* (white dog's-tooth violet), *Geranium maculatum* (wild geranium), *Polygonatum pubescens* (Solomon's seal), *Podophyllum peltatum* (May apple), *Smilacina racemosa* (false Solomon's seal), and, in the more sunlit grassy portions, *Antennaria canadensis* (everlasting), and *Galium* sp. (bedstraw). Claytonia, Erythronium, and Podophyllum, in particular, tend to form noticeable vernal socies.[4]

On the whole, most of the woodland gives evidence of being well-drained and in spots rather dry, as evidenced by the presence of such plants as *Poa compressa*, Antennaria, and Sassafras. Ecotones between the woodland and other types of habitat are in most places well defined.

The following vertebrates occur typically in the oak upland habitat:

Amphibians
- *Hyla v. versicolor* (Tree frog)

Birds
- *Buteo b. borealis* (Red-tailed hawk)
- *Corvus b. brachyrhynchos* (Eastern crow)
- *Myiarchus crinitis boreus* (Northern crested flycatcher)
- *Vireo olivaceus* (Red-eyed vireo)

Mammals
- *Sciurus niger rufiventer* (Fox squirrel)
- *Glaucomys v. volans* (Flying squirrel)
- *Tamias striatus lysteri* (Eastern chipmunk)
- *Peromyscus leucopus noveboracensis* (Northern white-footed mouse)

Of the above vertebrates the fox squirrel, white-footed mouse, and crow may be designated as predominants. All others of the indicated species are seasonals. The tree frog and chipmunk are inactive in winter, while the red-tailed hawk, crested flycatcher, and red-eyed vireo are absent due to migration.

Secondary Succession, a Xerosere

Plowed Ground.—As this is the initial stage in an important man-made succession, it is here ranked as a habitat in the sere. No discussion is needed.

Annual Weed and Cropland Habitat.—The acreage planted to annual crops varies somewhat from year to year, but averages about 60. Slightly more than one-half the farm (277 acres) has been cultivated, but much of this is usually kept in pasture or hayfields. As before mentioned, the cultivated fields lie on the east and north borders of the farm.

A cornfield most typically represents the annual weed stage in the succession from plowed ground and may be taken as a good example for description. The plants that first appear on newly broken ground are such annuals as

[4] The developmental equivalent of the society (Weaver and Clements, 1929). In this case a seasonal socies.

Ambrosia elatior (ragweed), *Amaranthus graecizans* (tumbling pigweed), *Chenopodium album* (lamb's quarters), and *Amaranthus retroflexus* (redroot). Grasses characteristic of the first season's growth are *Panicum capillare* (panic grass), *Setaria lutescens* (yellow foxtail), *Setaria viridis* (green foxtail), and *Eragrostis cilianensis* (stink grass). *Digitaria sanguinalis* and *Digitaria ischaemum* (crab grass) are often found on cultivated ground and in low fields *Echinochloa crusgalli* (barnyard grass) is apt to be common. Practically all of these ruderals produce fruits that are used as food by winter birds, thus making weed and croplands the most productive habitat from this standpoint.

It is commonly observed that the annual weed stage follows the breaking of the ground regardless of what the existing plant cover may be. It has been demonstrated that the seeds of these annuals are present in practically all soils, only awaiting favorable conditions to germinate. An experiment initiated by Dr. W. J. Beal in 1879 indicates that the seeds of some species may remain buried and viable for more than 50 years (Darlington, 1931). In Woburn barley soil Brenchley and Warington (1930) found more than 150 seeds of *Chenopodium album* per eight and two-thirds square feet. Chippindale and Milton (1934) demonstrated the seeds of annuals in the soil of permanent pastures that had not been cultivated for many years. That this phenomenon has an important influence upon animal life, particularly in winter, cannot be doubted.

Only one vertebrate species appears to make cultivated fields its permanent habitat. It is active during the entire year.

Peromyscus maniculatus bairdii (Prairie deer mouse)

Grassland Habitat.—The extent of this habitat can not be accurately stated. It increases as cultivated fields are allowed to revert temporarily to grassland pastures and diminishes as these are plowed for cultivated crops. Grassland is extensive and interdigitates with all the other habitats on the area. Probably one-fifth of the farm usually supports such cover.

The grassland habitat is very reflective of edaphic conditions. The better soils in this vicinity support a rank growth of *Poa pratensis* (Kentucky bluegrass). The dry, less fertile uplands are extensively occupied by *Poa compressa* (Canada bluegrass). Other grasses occurring commonly are *Dactylis glomerata* (orchard grass), *Cenchrus pauciflorus* (field sandbur), *Phleum pratense* (timothy), *Bromus tectorum* (downy brome grass), and several cultivated grasses that have been used for experimental purposes at the Kellogg Farm.

Some of the more common weeds found growing in grasslands are *Verbascum thapsus* (mullein), *Cirsium lanceolatum* (bull thistle), *Erigeron canadensis* (horse-weed), *Erigeron annuus* (daisy fleabane), *Plantago lanceolata* (buckhorn), and *Rumex acetosella* (field sorrel).

On the sanctuary ten years of constant pasturing by geese has practically eliminated the grass that formerly grew on the open slopes. As a consequence, these areas are almost entirely occupied by *Plantago lanceolata, Potentilla canadensis* (cinquefoil), *Hypericum perforatum* (Saint John's wort), *Erigeron annuus, Erigeron canadensis,* and a few other species of similar habit. The more dry and sterile soils where erosion has begun are in spots covered principally by the moss *Ceratodon purpureus.* Of the above species of plants *Erigeron annuus, Hypericum perforatum,* and *Erigeron canadensis* form well-defined seasonal socies in the order named from June until August.

The following birds and mammals characterize the vertebrate life of the habitat:

Birds

Otocoris alpestris praticola (Prairie horned lark)
Ammodramus savannarum australis (Eastern grasshopper sparrow)
Pooecetes g. gramineus (Eastern vesper sparrow)
Spizella p. pusilla (Field sparrow)

Mammals

Peromyscus maniculatus bairdii (Prairie deer mouse)
Microtus p. pennsylvanicus (Eastern meadow mouse)
Citellus t. tridecemlineatus (Thirteen-lined spermophile)

Of the above-named species all of the birds are absent part of the year due to migration. The spermophile hibernates. Thus the two species of mice are the only predominants.

Upland Brush Habitat.—The largest area of upland brush is a cut-over woodlot of seven acres which lies next to the woods on the north side of the farm. Other small or very sparse units are scattered here and there over the farm and sanctuary aggregating, perhaps, three acres. The habitat is one of the least extensive on the area.

Several species of woody plants characterize the upland brush habitat as it occurs on this area. In the well-drained sandy soil of the vicinity *Sassafras officinale* is almost sure to be present. *Rubus allegheniensis* (blackberry), *Rubus occidentalis* (black raspberry), *Rubus idaeus strigosus* (red raspberry), and *Rosa* sp. (rose) commonly form a thick tangle. One of the most typical trees of this type of cover is *Crataegus* sp. (hawthorn), and oak brush is likely to be an early invader. Over these trees, brush heaps, and through the briars a heavy growth of *Vitis vulpina* (wild grape) is frequently found. *Rhus copallina* (dwarf sumach) is often very common in such habitats.

In the seven-acre brush area on the farm the most common herbaceous species are *Poa pratensis, Pteridium latiusculum* (bracken fern), *Monarda fistulosa* (wild bergamot), and *Solidago* sp. (goldenrod). *Asclepias syriaca* (common milkweed) also occurs here.

A distinct type of upland brush in this region is *Rhus typhina* (staghorn

FIG. 7. The annual weed and crop-land habitat as illustrated by a corn-field in the fall of 1936.

FIG. 8. *Chenopodium album* (lamb's quarters) growing on cultivated ground. This plant produces quantities of food for seed-eating animals in winter.

sumach) which grows on grassy hillsides where insolation is high and conditions tend to be xeric. This species grows in pure close stands. It is seldom found mixed with other woody plants and is a poor type of cover for animal life.

The northern white-footed mouse *(Peromyscus leucopus noveboracensis)* is perhaps the most characteristic animal of this habitat. It is active throughout the year.

Upland Woods Habitat.—Invasion of the upland brush by oak and hickory eventually results in its displacement by the upland oak woods. This habitat has already been described.

Artificial cover types

Coniferous Plantations.—In 1927, when the area was purchased, large plantings of conifers were made on the 80 acres of the sanctuary and the hilly parts of the farm adjoining to the east and to the west. The stands vary in extent from a few scattered trees to five acres of massed pines. The species most commonly used were Scotch pine *(Pinus sylvestris)*, red pine *(Pinus resinosa)*, white pine *(Pinus strobus)*, and white spruce *(Picea canadensis)*. Smaller numbers of Austrian pine *(Pinus nigra austriaca)*, western yellow pine *(Pinus ponderosa)*, and Norway spruce *(Picea abies)* have also been used. On the sanctuary small clumps of white cedar *(Thuja occidentalis)* and ground juniper *(Juniperus communis depressa) were planted.* Approximately 20 acres have been planted to conifers and the plantings are scattered over an area of about 100 acres, extending from west to east across the farm and including the sanctuary.

The coniferous plantations were made, for the most part, in grassland, and this cover type is present wherever the pines are spaced far enough apart for any other plants to grow. The most characteristic animal of the smaller spruces and junipers is, perhaps, the chipping sparrow *(Spizella p. passerina)*. The large trees are a favorite nesting site of the eastern mourning dove *(Zenaidura macroura carolinensis)* and the eastern robin *(Turdus m. migratorius)*. The white-footed mouse is also commonly found here.

Deciduous Plantations.—In the summer of 1935 a study was made of cover distribution on the Kellogg Farm by the Michigan Department of Conservation. Banks, gullies, edges, and corners of fields over the farm were fenced off and planted to oversized nursery stock. Most of the species used were food-bearing shrubs. Some of the genera most commonly represented were Cornus, Viburnum, Berberis, Amorpha, Lonicera, Symphoricarpos, Ligustrum, Rosa, Ptelea, Morus, and Eleagnus.

During the severe drouth of the 1936 growing season these plantings made poor progress and many of the shrubs died. For the period of this study the planted areas have not been an important habitat type and hence can be

passed over with little comment. These shrubs are ideally situated to improve the cover distribution of the farm, but their growth to date has not been sufficient for them to serve an important function in this respect.

SEASONAL CHANGES

In order to convey a clearer impression of the changes which this animal environment undergoes it will be well to review briefly the main differences in its seasonal aspects.

In summer the area is characterized by very dense cover everywhere. The vigorous plant growth of this season provides a plentiful basic food supply for herbivores and through them, all other species. Insects, frogs, and other forms are abundant, and the young of all species are present as food and as the consumers of food. The capacity of the area for supporting life reaches its height in summer. Although the numbers of animals present and their activity are at a maximum, the observation of terrestrial forms is extremely difficult due to the sheltering greenery that is everywhere.

In the autumnal aspect the green of summer is gone. Killing frosts have reduced herbaceous vegetation, though it is still important as cover. In wooded areas the ground is thickly layered with leaves. The chief characteristic of autumn, however, is the tremendous abundance of mast, fruits, and seeds. All this does not remain to support resident winter populations, since large flocks of migrant birds demand a large food supply. The foods that are present in fall depend to some extent upon the nature of the growing season that went before. However, abundance is the rule despite the fact that insects are rapidly disappearing at this season and many of the "cold bloods" are becoming inactive.

In winter a variety of conditions may exist; but there is usually considerable snow on the ground in this region, which effects material changes in ground cover. Under deep snow herbaceous vegetation becomes of very minor importance. Thick brush, conifers, or holes in the ground become the retreat of species that need such protection. Large open areas that supported abundant life in summer appear to be deserted in winter. Animal populations and food supplies diminish to their lowest point late in the season, although the early melting of snows may increase the availability of foods to some extent. Winter is the season of the progressive destruction of what the summer has produced.

In early spring vegetation has reached its lowest point, although the disappearance of the snow renders available as cover the more enduring herbaceous plants of the summer before. This absence of snow also makes possible the gleaning of the last remnants of the fall abundance of fruits and seeds. As new plants begin to grow, insect life awakens, and many species start to breed. Gradually, with the advent of migrant birds and the increasing vegetation, the activity of summer is resumed.

ANIMAL LIFE OF THE AREA

The widely varying habitats of this portion of Michigan support correspondingly different animal populations. The biota of a creek bottom will be found to differ materially from that of an upland farm in an adjacent section of land. Although the region as a whole presents a heterogeneous pattern of distinct communities, nearly any 10-mile square will be found to contain a large portion of the vertebrate species occurring anywhere in southern Michigan.

In the appendix is given a list of all the vertebrates recorded on the Kellogg Farm during three years. Alone, this check-list would present a very poor picture of the associated species living here. Several of the animals listed have been recorded only once on this area, although they may be common within a few miles. In neighboring creek bottoms, in particular, the fauna contains many species not found on the Kellogg Farm. In a glance at the list of Amphibia a conspicuous lack of salamanders is noticed. Only one salamander *(Ambystoma maculatum)* has been recorded in three years, although a particular effort was made to find more. There is only one record of the pickerel frog, which is common around near-by spring-fed streams. The green frog and wood frog are present in only small numbers, while the leopard frog is very plentiful. The Fowler toad and the American toad are both common. Snakes are not numerous on the farm, the ribbon snake probably being most frequently seen. Turtles are abundant both in the lake and in the swales. The list of birds for the area is very complete in the case of waterfowl and sparrows, but is limited for warblers. The sparrow hawk is not often seen, though it is common a few miles away. The swamp sparrow, Henslow sparrow, indigo bunting, and short-billed marsh wren are seldom observed on the area, although they may easily be found in certain habitats not far distant. A red squirrel has been found on the farm only once; yet two miles to the east it is common in the tamaracks around Augusta Creek. The only record for a fox[5] was in February, 1937, when one animal left tracks on the area for several nights. No star-nosed mole has been captured during this work, but one was taken here in 1933. Bats have been seen at the sanctuary but none collected. Only two pine mice and one least shrew have been taken in three years. The animals of infrequent occurrence are probably of little significance in the bionomics of the area, and they need be little more than mentioned here.

POPULATION STUDIES ON CERTAIN ANIMALS

In the following pages will be given the results of an attempt to ascertain the numbers present of the species of resident upland birds and mammals. The work has been most nearly complete for the cottontail, fox squirrel, skunk, opossum, pheasant, and quail. Data on hawks and owls are restricted to field observations.

[5] The red fox recorded in the check list was identified on the basis of these tracks. There was little doubt that the animal was this species as the gray fox is very rare in this region.

METHODS

The census methods used on the larger mammals varied somewhat and are discussed under the several species. In general, trapping and marking have constituted a basis for the work. A line of from 20 to 70 box traps (fig. 9)

FIG. 9. Box traps covered with third-inch-mesh hardware cloth were used in taking the larger mammals.

was run from October to April during both winters of the study. Figures 10 and 11 give the distribution of traps during the two winter seasons. Traps were placed, for the most part, in brush cover, as this was particularly desirable from the standpoint of the rabbit study. The baits used were an ear of corn and half a chicken. The corn attracted rabbits, squirrels, pheasants, and quail. The chicken was an efficient bait for skunks, opossums, and house cats. Both baits usually were used in each trap set.

Pheasants and quail were censused by traversing the area with as many men and dogs as were available. The numbers of men used varied from 5 to 12, and there were usually from 1 to 4 dogs. Every part of the farm was included, the more dense cover being worked most intensively. Birds flushed were marked down and duplicates avoided as much as possible. This method

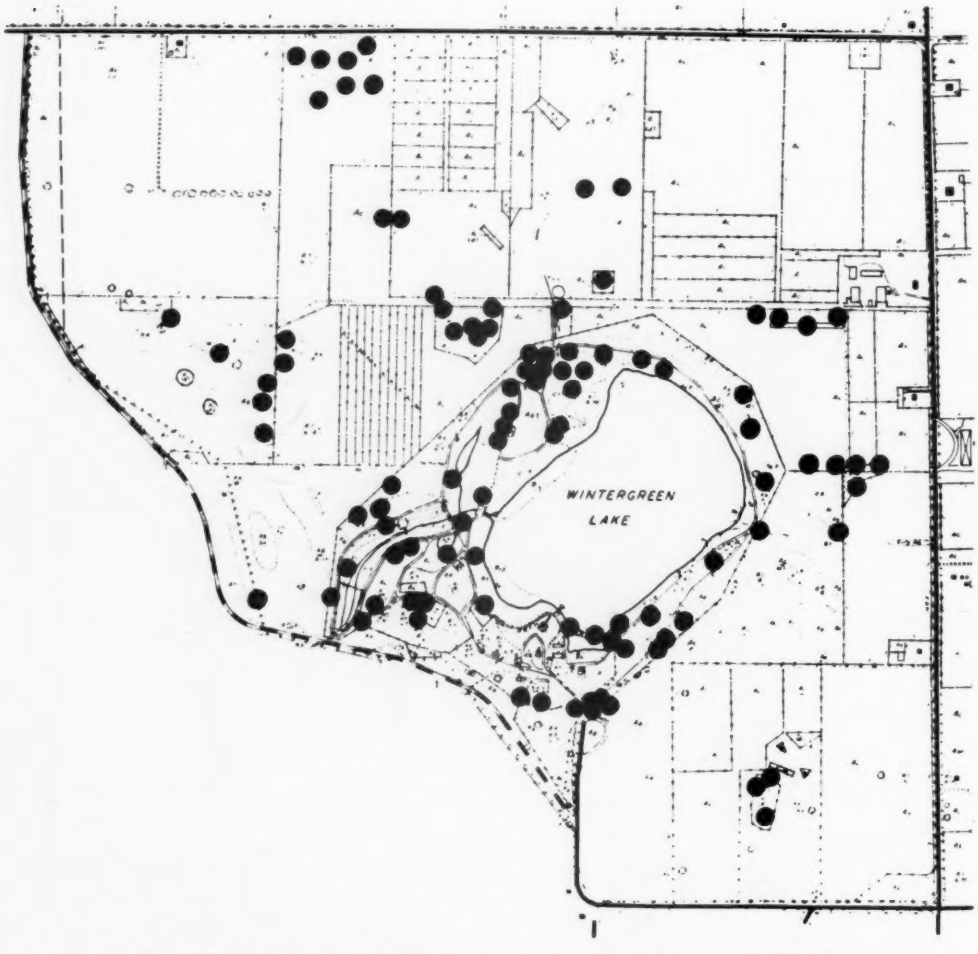

FIG. 10. Distribution of box traps during the winter of 1935-36.

was by no means perfect; but a repetition of such censuses, together with regular field work and the results of trapping and banding, appear to have given a fairly accurate indication of the number of birds on the area.

The habitat preferences and relative abundance of mice and shrews were ascertained by operating a line of 200 ordinary mouse traps during fall, winter, and spring, as time allowed. The traps were set three feet apart and baited with peanut butter. The work of Townsend (1935) indicated that peanut bait would be acceptable to all of the species present here. Field observations on tracks, burrows, and nests also were useful indices of the abundance of small mammals. The population numbers of these animals are indicated only relatively.

In giving numerical values to animal populations it is necessary to state the time of year for which a census is calculated. Populations are being continuously augmented in the spring and summer breeding season and steadily reduced in winter. Nearly all of the figures for the area studied represent

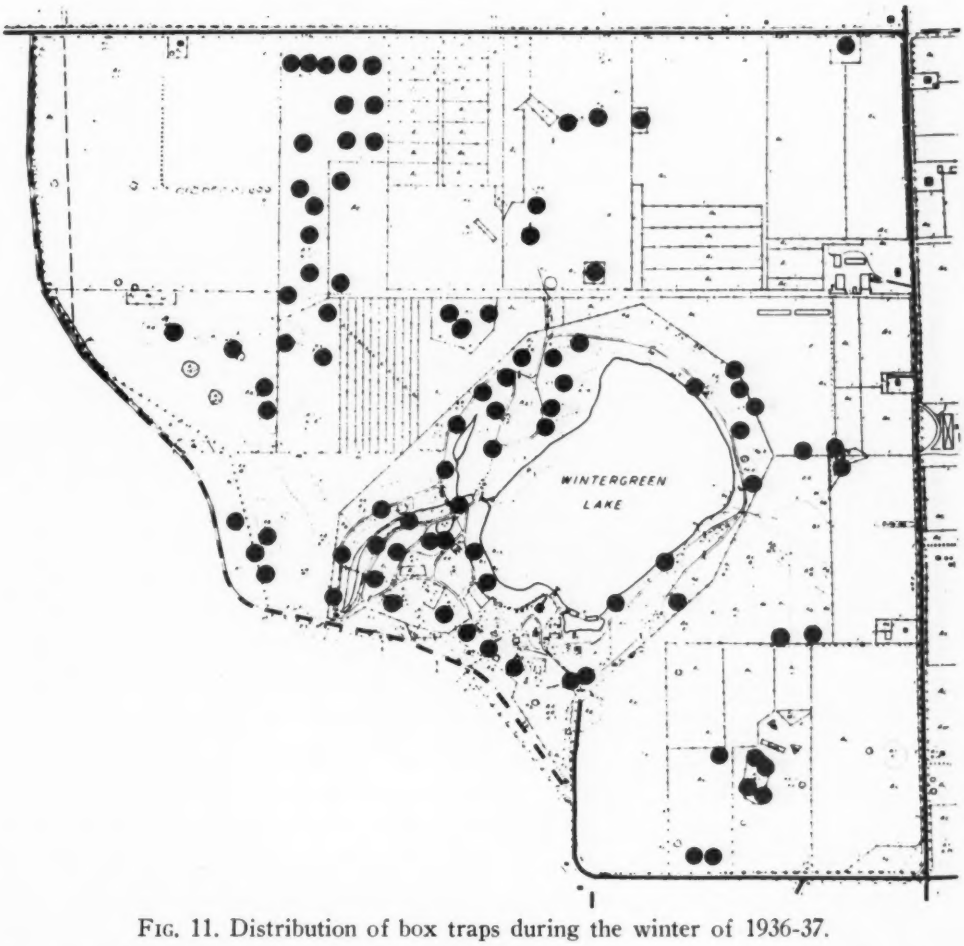

FIG. 11. Distribution of box traps during the winter of 1936-37.

the winter season. For most species it has not been possible to be more specific than this, but for rabbits a definite date is given. Population figures are, of course, only approximate.

LARGER MAMMALS AND BIRDS

Cottontail Rabbit

The section of land here treated has been known for many years as good hunting territory for cottontails. The increase in the natural coverts since 1927 and the planted conifers appear to have made the area even more favorable to this species.

Technique.—After preliminary experiments with apples, oatmeal, wheat, and scratch feed, it was found that the best bait for rabbits was an ear of corn. The chief advantage of this bait was that it was not carried away by mice nor easily covered up by snow. Intensive rabbit trapping was started on January 1, 1936. At this time it was apparent that rabbits had gathered into cover patches all over the farm. Hence traps were confined, for the most part, to these locations (fig. 10). As tracks were nearly absent from open

fields and less than 30 traps were available at this time, it was necessary to use the latter as effectively as possible. Throughout these studies traps have been placed where signs showed rabbits to be most plentiful. As the trapping was confined chiefly to late fall and winter, the greater part of it was done in deciduous brush, coniferous plantations, planted washes, and dumps, where rabbits were most numerous at this season. Table 1 gives the summarized rabbit trapping data for the entire study.

TABLE 1. SUMMARIZED RABBIT TRAPPING

Period	Trap nights	Individuals handled	Repeats	Total catch
December, January, February, March, 1935-36 ...	3,342	70	366	436
October 31 - December 17, 1936	2,045	102*	96	187
January, February, March, 1937	5,289	24	94	106
Totals	10,676	182**	556	729

*Including repeats on some rabbits marked in former trapping periods.
**The rabbits marked formed a numerical series from 1 to 181. There was one uncorrected duplication that makes the total number of individuals 182. Several rabbits were taken by methods other than trapping and so are not included in the total catch by trapping; they are, however, represented here in the total of marked rabbits.

In this study rabbits were marked by tattooing a number on the inside surface of the right ear. The rabbit was placed in a small cloth bag and the ear slipped out through a hole. A sharp pen was dipped in black carbon ink and the number stippled in by puncturing the skin. Such numbers were permanent and easily read.

Census of December, 1935.—In 1935 rabbit shooting began at the sanctuary and farm on December 3. During the month of December a total of 154 rabbits were killed on the 500 acres. In the trapping period from January 1 to March 31 individual rabbits taken and marked numbered 63. In addition to these, 11 more unmarked rabbits were recorded as mortalities.[6] Hence 228 individual rabbits were handled. If there was no general movement of rabbits onto or from the area during the period of the shooting and the period of trapping, the number of animals given represents a minimum population figure. For those who consider "hunting pressure" as a force tending to drive rabbits off the farm, it is to be pointed out that most of the surrounding land was also being hunted. On the other hand, for those who may consider the hunting on the farm as tending to evacuate favorable habitats which might be filled by an influx from outside, it must be remembered that an apparently similar reduction of the population density was taking place outside the area. Range records show that there is a marked tendency for individuals to remain in a given locality when the ground is covered by snow in the winter. There is no indication of a trend of movement onto or from the farm. There is, however, no actual proof that such a movement did not take place, and this is a possible source of error that may be evaluated in a number of different ways.

[6] Three additional mortalities in which the ears were eaten by predators were probably marked animals (from circumstances). They are not added here as it is likely that they are already included in the total of 63. There is a possible error of three in the total of handled rabbits.

TABLE 2. RABBIT TRAPPING BY MONTHS; WINTER, 1935-36

	December*	January	February	March
New rabbits caught	3	37	15	8
Total individuals handled (old and new)	3	39	44	27
Total repeats	0	85	197	84
Trap nights	12	608	1,064	1,658

Individuals caught on Farm....63
Individuals caught on Kellogg Eestate....7

Total rabbits marked to April....70

*Only three days' trapping included.

If it is postulated that rabbits were not driven off the farm by shooting and did not gravitate to the area to occupy desirable habitats in which the population was reduced, the main question regarding this type of census is whether or not a large percentage of the rabbit population was handled. Table 2 shows that during January, plus three days in December, 40 rabbits were marked. In February the number of new rabbits caught declined to 15. In March the number of new rabbits dropped to eight. A progressive decline in the number of new unmarked rabbits caught is to be expected as more and more of the population are marked. The fact that only eight new animals were taken during March indicates that the trapping job had accounted for a large portion of the rabbits on the farm. As shown by fig. 12, however, the efficiency of traps dropped significantly during March, and this fact must be considered in evaluating the results. It is not possible to say how many unmarked rabbits remained after April 1. It seems probable, however, in the light of subsequent work, that if this number were known, our minimum population figure of 228 would not be increased enough to alter greatly conclusions as to the status of the species on this area. Probably a more reliable basis for judging the census is obtained from the results of an entirely different type of population count taken during the following winter season.

Census of December, 1936.—In the fall of 1936 facilities were at hand for a census employing the "banding returns" principle which Lincoln (1930) suggested could be used in calculating the abundance of American waterfowl. The plan was to mark as many rabbits as possible over as short a period as possible. Immediately, then, a large number would be shot. From the percentage of marked rabbits in the kill the total population might be calculated. The relationships of the quantities may be expressed by the formula, $A/B = C/X$, in which X equals the total rabbit population and C equals the number of rabbits marked. A and B equal the marked rabbits shot and the total rabbits shot, respectively.

Accordingly on October 31 trapping was begun in the winter coverts (fig. 11, p. 371). During the following six weeks 92 rabbits were trapped and marked. In addition, eight rabbits were taken which had been marked during the preceding winter, and two which had been taken in a box trap set

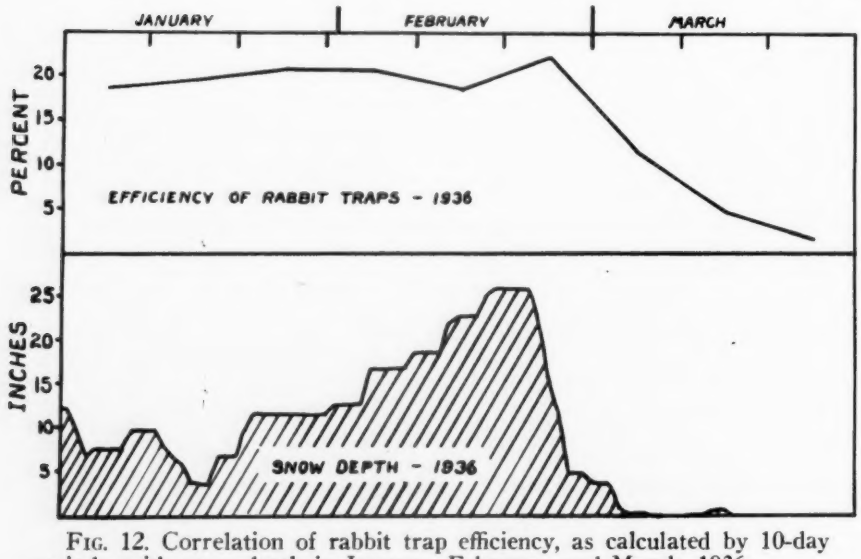

FIG. 12. Correlation of rabbit trap efficiency, as calculated by 10-day periods, with snow depth in January, February, and March, 1936.

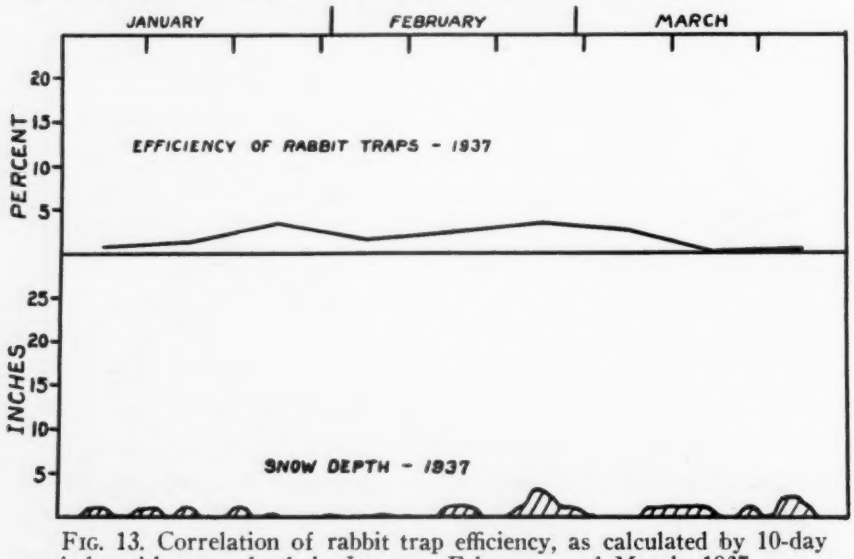

FIG. 13. Correlation of rabbit trap efficiency, as calculated by 10-day periods, with snow depth in January, February, and March, 1937.

for cats on the sanctuary a few weeks previously.[7] Thus a total of 102 marked rabbits were known to be alive during the period of six weeks and six days.

TABLE 3. RABBIT TRAPPING BY MONTHS; FALL AND WINTER, 1936-37

	November	December	January	February	March
New rabbits caught	70	22	9	2	1
Total individuals handled (old and new)	73	61	21	19	7
Total repeats	25	71	27	47	20
Trap nights	979	1,066	2,021	1,820	1,448

Individuals caught on Farm (in this period).....114
Total rabbits marked to April 1.....181

[7] Several such traps were operated at various times and the few animals caught were turned over to me for marking.

On December 18, 19, and 20, in a systematic hunt covering the entire area, 126 rabbits were shot. As rabbits were killed the locations were marked on a map in the field (fig. 14). In the total kill 57 rabbits were found to be marked. The total population, then, was calculated as follows:

$$\frac{A}{B} = \frac{C}{X} \quad \frac{57}{126} = \frac{102}{X} \quad X = 225.4 \text{ rabbits}$$

Probably the most uncontrollable variable in a census of this type is the unrecorded mortality (and possible movement) that occurs among the marked animals during the trapping and shooting period. The shorter the period can be made the smaller will be this error. In the present census this figure amounts to what mortality occurred among a number of rabbits that progres-

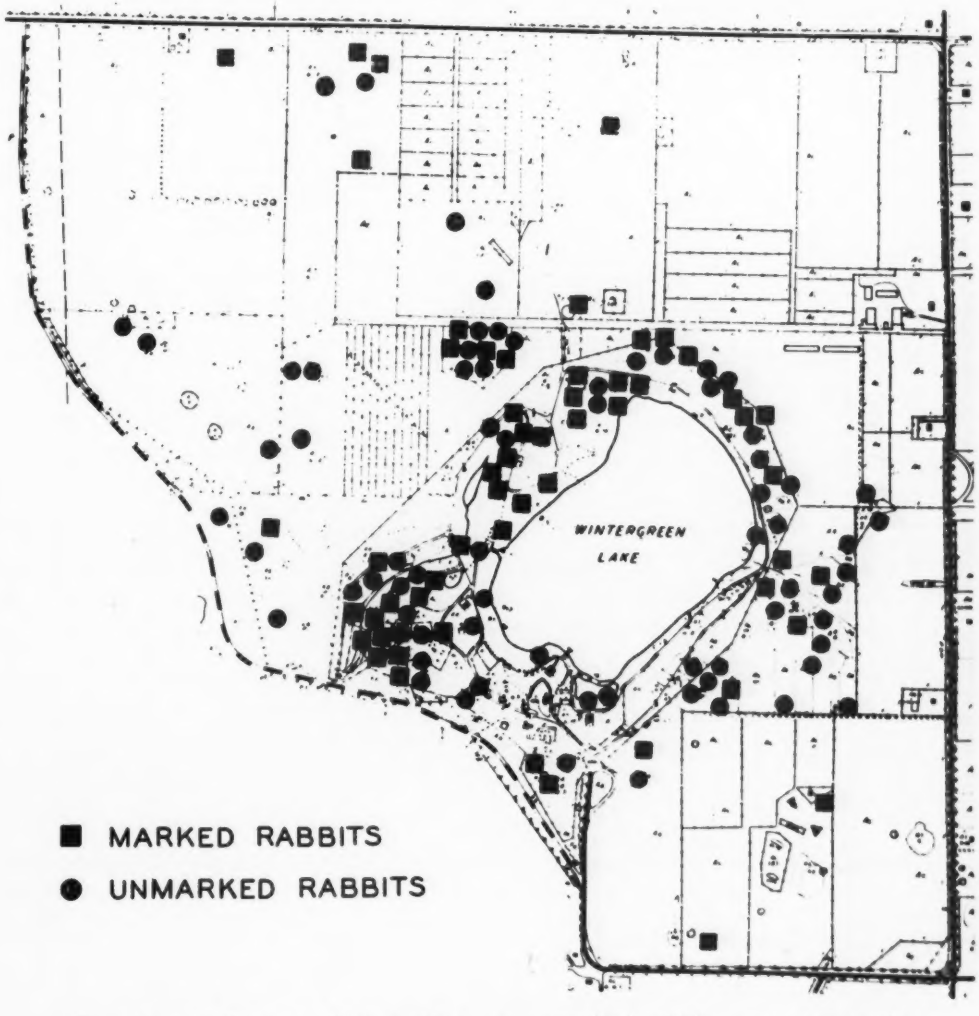

FIG. 14. Locations at which marked and unmarked rabbits were shot in the census of December 18, 19, and 20, 1936. Through an error in the field one unmarked rabbit is recorded here that could not be accounted for when the kill was examined.

sively increased from 1 to 102 in seven weeks. This is probably the greatest unknown in the census.

There are, however, other possible sources of error in this type of census. If any part of the farm had been intensively trapped and not intensively hunted, the indicated relationship of the members of the proportion would not be true. Also if any important rabbit habitat had not been trapped, but had been hunted, a similar error would be introduced. These possible inaccuracies were anticipated and every effort was made to include all of the rabbit habitats in both the trapping and shooting. It is believed that this was very efficiently carried out. On the map in fig. 14 are given the locations where every marked and unmarked rabbit was taken.[8] A comparison of this map with that giving trap locations (p. 371) will show that there was little disparity between the areas trapped and those shot over. If there was no great inequality one way or the other, it is quite probable that the minor errors of judgment would tend to cancel out. As for the mathematical errors of the count, these are dependent upon the size of the population and the percentages of the rabbits that were marked and shot. The population appears to have been about 226 animals; and of these 45 percent were marked, and 55 percent were shot. It is improbable that sufficiently large mathematical errors occurred to distort seriously the result.

Evaluation of Winter Inventories.—In considering the two census methods used it is evident that the one employed in the fall of 1936 is the most reliable. During the first winter of the work, trap efficiency was high (fig. 12). This is correlated directly with deep snow, which concentrated rabbits in cover patches and probably rendered the bait more attractive. Thus it was possible to handle a large part of the population, and what appears to be a good approximation of the number of animals present resulted. The census of the following fall showed the population to be much the same, but the winter that ensued was a season of little snow and comparatively high temperatures. Trap efficiency was low. Since, of the 226 rabbits indicated to be on the area, 126 had been killed in the census and 10 more had been shot in December hunting after the census, there were probably about 85 rabbits (allowing a few for animals shot but not retrieved in the hunting) on the area. Yet of this number only 27 individuals were handled in the next three months (as compared with 63 the winter before). Obviously the efficiency of the method first used depended upon weather conditions and would have been entirely inaccurate during the second season. The marking ratios method, however, was dependent upon traps only during seven weeks in November and December. During this period, despite a lack of snow, the bait in the traps was attractive to rabbits. The fact that the population was considerably more than 50 percent higher than it was late in the winter also probably contributed much to the efficiency of the traps and the success of

[8] These locations indicate, in all possible cases, where the rabbit was flushed. Where this was not definitely ascertained, the location at which the animal was first seen was used.

the method. From the results of this study the marking ratios method appears to be a reliable one for censusing rabbits on areas such as this.

In comparing the results of the two censuses for these two years a close approximation is obtained. In 1935-36 the census (calculated as of December 3) indicated 228 + rabbits. In 1936-37 an entirely different type of census (calculated for December 18) gave a result of 226 rabbits.

The fact that there was a difference of only two rabbits between the two counts does not, of course, indicate a proportionate accuracy in the censuses. Probably any one of the errors involved in either method is large enough to produce a greater discrepancy than this, even if the populations had been the same. The fact that the two census figures would fall within nearly any estimation of the values of the errors involved in each is the point of real significance. Since the second census was not subject to the most important unknown of the first (i.e. an unknown unhandled surplus of rabbits and the possibility of movement during the long trapping period) it may be considered, in a limited degree, a check on the first method. There is no guarantee that the populations were nearly the same, but there was no apparent difference in the numbers of rabbits present in the two years as judged by field observations during the hunting period.

As to the possibility of using other census methods, no other system proved feasible in this study. Attempted censuses with dogs proved to be hopelessly inadequate. Springer spaniels were used on bird censuses and the highest number of rabbits seen in a day of field work covering the entire area was 21. If enough men are used to drive cover patches, the possibility of counting individual rabbits several times is high. In addition, rabbits that are holed up will not be counted. Droppings and tracks have been useful indices of abundance in comparing habitats, but for estimating actual population numbers over a large territory, they have in the present case been found to be entirely unreliable. These results are in keeping with those of Trippensee (1934). He tried similar methods, which are described as (a) the sample area pellet count, (b) dog-census, (c) man count, and (d) track-feeding method. None of these was found to be satisfactory.

Spring Population, 1936.—The best clue to the size of the spring population on the Kellogg Farm comes from the trapping of February and March, 1936. An index may be obtained from the number of individual rabbits handled (and thus known to be alive) during this period of 60 days. Some rabbits doubtless escaped handling and some mortality (in rabbits counted) probably occurred. The difference between these two opposing errors is the real error.

In the trapping of February and March, 45 individual rabbits were handled (including both rabbits newly marked and old repeats). During most of February, trap efficiency was high, averaging near 20 percent. Rabbits were concentrated in cover patches where the box traps were located. When, how-

ever, the snow melted late in that month, rabbits apparently spread out and more green foods became available. Trap efficiency dropped to around 2 percent and continued low throughout March (fig. 12). Thus the chances of a rabbit's being handled after late February were considerably diminished, although during most of that month they were good. Considering these facts, and allowing a few for mortality, it seems likely that the April population of cottontails was near 50, or 25 pairs of potential breeders.

Productivity of Land.—If the above figures are used, a December (1935) population of near 228 cottontails furnished a hunting season kill of 154 and left a population which on April 1 was about 50. This spring breeding stock produced a December population of near 226. Of these, 136 animals were shot and approximately 85 were left, out of which another spring breeding stock would survive. In terms of land units the Kellogg Farm during these two seasons has in December supported one rabbit per 2.1 acres.[9] It appears to be possible for this area to produce consistently a hunting season crop of about 150 rabbits, or one rabbit per 3.2 acres of land.

Seton (1929) states, "It is established that no wild animal can stand a heavier drain than 20 per cent. per annum of its total numbers." Based upon this and using the estimated annual kill (100,000,000) he calculates the total population of the United States to be not less than 500,000,000 cottontail rabbits. Although the above conditions may hold for the country at large, it appears to be possible for a local population to support a considerably larger annual kill than that indicated. Unless the figures presented for the Kellogg Farm are subject to a much larger error than they appear to be, the population here has endured an annual toll of more than 50 percent. However, there may be conditions here, such as the large amount of coniferous cover, that render the area somewhat exceptional. This can be judged only when similar work is done on different territory.

Summary.—Box traps baited with an ear of corn were used in capturing rabbits. Under conditions of deep snow, trap efficiency was about 20 percent. Certain individual animals were inclined to develop trap habit. In one case a rabbit was taken 30 times in slightly more than two months. Rabbits were marked by tattooing a number in the right ear. By adding the total December kill to the total number of rabbits handled in the traps during January, February, and March, a minimum population figure of 228 rabbits was obtained for the winter of 1935-36. In December, 1937 a census by the "marking ratios" method indicated a population of 226 rabbits. The second census method was found to be the more reliable as it is not so much dependent upon weather and indicated a true population figure rather than a minimum one. The spring rabbit population (1936) of the Kellogg Farm was probably near 50. The December population density was apparently one rabbit per 2.1 acres. It is indicated that this area can consistently produce a hunting season crop of 150 rabbits, or one animal per 3.2 acres of land.

[9] On a basis of 480 acres of land (i.e. allowing for Wintergreen Lake).

Fox Squirrel

Oak openings in the primitive forest evidently were a most congenial habitat for the fox squirrel. It is not surprising to find the species common in this region where even yet, for an agricultural district, a comparatively large portion of the land is in oak woodland. The grazing of woodlots probably harms the fox squirrel less than any other game species.

Technique.—In the present investigation it was not possible to employ optimum trapping methods on every species dealt with. A much better study could have been made on the fox squirrel had this been the only consideration. These animals were taken in the box traps baited with ear corn. Although comparatively few traps were placed directly in oak woods, the extent to which squirrels travel on the ground rendered them comparatively efficient. The open wire trap is not well adapted to the handling of this species. These animals often fight furiously to break through the hardware cloth and sometimes succeed at the expense of torn claws, worn teeth, and a badly scratched head. Squirrels are very susceptible to shock and exposure to severe weather. As a result, many mortalities occur. In a total of 161 times that squirrels were handled in traps on the Kellogg Farm, 21 individuals were found dead.

During the first winter of the study these animals were marked by cutting a large V in the right ear. This did not designate individuals but merely indicated that the animals had been taken previously. During the second year individuals were marked by clipping a toe or a combination of two toes. Neither method is to be recommended. Ear notches in some marked squirrels appeared to heal over in a year until it was not possible to make sure the animals had been handled. Although there was no observed incapacity in toe-clipped animals, it would seem advisable to find a different method for an arboreal species.

Numbers Present in 1935-36.—During this winter fox squirrels were very abundant in the oak woods of the farm and sanctuary. In the winter trapping period 52 individuals were marked and 9 unmarked animals were recorded as mortalities. Thus 61 squirrels were handled, and this is an index figure for the early winter population. It is not certain that all of the squirrels were caught, nor is there any guarantee that all of those caught were resident within the limits of the Kellogg Farm. Tracks indicate that half a mile is no great distance for a squirrel to travel, and animals from Midland Park might well have been taken in the traps.

Numbers Present in 1936-37.—Due, evidently, to the action of a serious epizootic[10] in the spring and summer of 1936, the squirrel population in the fall of that year was considerably lower than in 1935. On the farm, squirrels

[10] A mange-like disease probably identical with that described by Errington (1933) appears to be endemic among the squirrels of this vicinity. In the spring of 1936 it appeared to spread widely among this species on the Kellogg Farm and in Midland Park. Numerous animals were seen with patches or nearly all of their hair missing, and several sick and dying squirrels were observed and others reported. An examination by Dr. Don R. Coburn, then pathologist of the Game Division, Department of Conservation, revealed no cause for the condition, which took the form of a severe dermatitis accompanied by extensive exfoliation of the skin.

were seen much less often, and in Midland Park the comparative scarcity of the species was even more manifest. The cottages in Midland Park are built among a uniform growth of oak trees. Protection from shooting has been practically complete, and squirrels have become very common. Any difference in numbers is readily noticed by residents here, and reports in the fall of 1936 were unanimous in the opinion that the number of squirrels had markedly decreased. Although from 20 to 40 box traps were operated from November 1 to December 18 on the Kellogg Farm, squirrels were caught only 8 times. However, this may have been partly due to the abundance of fall food (notably acorns) which made the corn in the traps less attractive. For the entire trapping period 24 individuals were marked and liberated and 15 unmarked squirrels were recorded as mortalities. The index population figure, then, is 39.

Evaluation of Data.—Considering everything, the figures 61 and 39 can be taken as fairly good indices of the numbers of animals present in the two seasons. The fact that more traps were used and more set in the woods during the second season would tend to neutralize any reduction in efficiency of operation resulting from the open winter. The fact that there were six weeks of trapping in the fall of the second season also tends to swell the total for that year. Any discrepancy in technique appears to be in favor of the 1937 period. However, the variables involved are too many and too little understood in the light of squirrel behavior to justify a more specific attempt to correct these figures.

Few population figures relating to squirrels have been found in the literature. One is cited by Seton (1929). Near Austin, Texas, in a "squirrel bush" of oaks, pecans, and red elms, an area of about 100 acres was alleged by a game warden to have a population of probably 500 fox squirrels. If this estimate and the figures given above for the present area are at all reliable, it would seem that even what appeared to be an abundance of squirrels at the Kellogg Farm in 1935 is not necessarily the maximum population density that the species may reach under some conditions. In the Texas area the population was about five squirrels per acre, while at the Kellogg Farm in the fall of 1935 the population was (on the basis of 61 squirrels and 30 acres of woodland) 2 squirrels per acre. As fluctuations appear to be an invariable characteristic of rodent populations under natural conditions, each of these figures can be taken to represent a temporary condition only. The true productivity of a habitat must be calculated by averaging the population numbers for a large number of years. For some sample areas in Missouri Bennitt and Nagel (1937) found that the maximum population density was one squirrel per 2 acres of woodland. They add that "—such a heavy concentration seldom occurs." For the southern half of that state they found that one squirrel per 8 acres was a fair average. Presumably these sample areas were open to hunting, and the numbers given may be applicable to similar conditions in

Michigan. Appearances seem to indicate that such a concentration as that of 1935 on the Kellogg Farm seldom occurs under ordinary conditions where the animals are hunted.

Eastern Skunk

Of the type of habitat favored by the skunk, Seton (1929) says, "—he loves variety—dry, rolling land, well watered, and alternated with sun and shade. In open fields, mixed with dense cover, he finds his ideal home." This might indeed be a description of the area around the Kellogg Farm, which certainly is very favorable to this species. Mr. William Parks, fur buyer in Augusta, reports that this area produced an excellent yield of skunk furs each season for many years before the establishment of the sanctuary. From 1927 to 1931 intensive predator control was practiced at the sanctuary and many skunks were killed. After that time smaller numbers were taken until the fall of 1935. During this investigation none was killed on the farm between the spring of 1935 and when animals were taken for breeding studies in 1937.

Technique.—Preliminary experiments during 1934 and 1935 showed that in fall and winter fresh carrion was an efficient bait for skunks. At the large poultry plant of the Kellogg Farm dead chickens were nearly always available. Hence the bait for box traps was standardized at one-half of a chicken. The box traps used were, in general, well adapted to the taking of skunks. Their chief disadvantage lay in the fact that skunks would, at times, tear a hole in the hardware cloth and escape. For skunks alone heavy-gauge, inch-mesh poultry wire would be preferable as a trap covering.

During the 20-month period from October, 1935 to June, 1937 a total of 143 individual skunks were handled on Section 8 or near-by. Of these, 83 were taken for the first time in box traps, 22 were dug from burrows, 31 were caught in steel traps, and 7 were found dead on the highway or elsewhere. Live skunks were handled 191 times and were taken in box traps a total of 165 times. The largest number of repeats for any individual was 6, and the average was 1.7.

Skunks were handled by covering the trap with burlap and dumping the animals into a bag. They were removed from the bag and manipulated by a hold on the base of the tail and the back of the neck. Marking as individuals was done by toe clipping and was satisfactory except for the tendency of skunks to lose toes in traps. There were a few cases of uncertain identity on this account.

Numbers Present in 1935-36.—The first skunk was captured on October 21, 1935. On January 2, 1936 the fourteenth skunk was taken. During the very cold winter weather no skunks were caught in the traps, and the next animal appeared on February 26. From then on skunks were taken regularly, and by April 12 a total of 30 different animals had been trapped and marked.

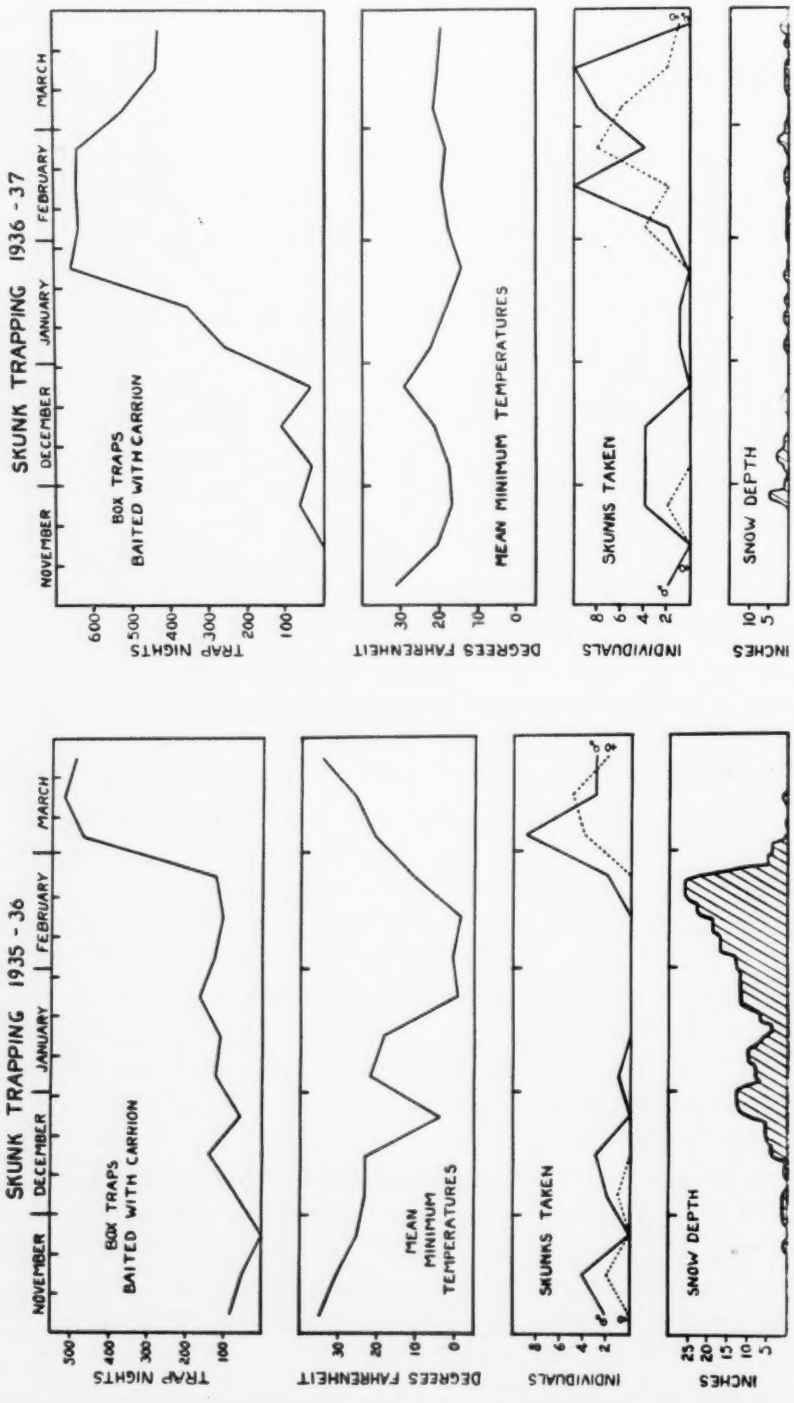

FIG. 15. Male and female skunks taken in box traps as correlated with temperature and snow depth in the winters of 1935-36 and 1936-37. Trap-nights, temperature, and skunks trapped are calculated for 10-day periods.

All of these were caught on the Kellogg Farm. Thus at least 30 different skunks were known to have been on the area during this period of 5½ months.

Upon examination of the sex ratio in this group of skunks, however, it was found that only ten were females. Subsequent work showed that a pre-

ponderance of males are handled in winter, due to a differential inclination between the sexes to remain holed up during cold weather. A similar condition was found by Cuyler (1924) in Texas and by Hamilton (1937a) in New York. In the 143 skunks handled in this study there were 79 males and 64 females, or a ratio of 0.447 females of the total population. It appears that there are fewer females because most of the animals were taken in winter when females were relatively inactive. Of 16 skunks handled from July to October (1936) 8 were males and 8 were females. In the light of these indications and subsequent results, it appears that the actual sex ratio here is 0.5.

Since 20 male skunks were captured over the winter, an equal number of females (presumably holed up much of the time) may, perhaps, be assumed; therefore a total of at least 40 skunks is indicated. This figure is not so well substantiated as would be desirable, but it is the best indication available of the number of animals which to a greater or lesser extent occupied the area during this period.

Numbers Present in 1936-37.—From September 17, 1936 until March 22, 1937 traps took 29 individual male skunks and 15 females on the Kellogg Farm (sex ratio, 0.34). During this season, however, 19 burrows (selected for appearances of occupation) were excavated, and these accounted for 2 males and 16 females that had not been handled previously in this trapping period. Thus the total catch was 31 males and 31 females (sex ratio, 0.5). Just what constitutes a "resident" skunk is difficult strictly to define, but as used here the word refers to animals that were using burrows on this area. Doubtless some of the skunks caught ranged in part over this area, although their customary burrows were elsewhere. This is supported by the fact that of 8 of the animals marked here 5 were retaken in the "turkey marsh,"[11] 2 in Midland Park, and one was followed to a burrow at nearby Duck Lake.

Since an intensive job of trapping was done during the early part of 1937, it appears probable that a large part of the male animals ranging over the farm were caught. The best indication of resident skunks, however, (not animals using the area, as was calculated for the previous season) comes from the females taken from burrows.

More than fifty burrows were watched during the winter, and it is fairly certain that those were excavated about which the most skunk signs occurred. As a number of females were in some cases concentrated in a single burrow (table 4) it appears that a few dens on the area contained most of the resident animals of this sex. In all, 22 females were accounted for by digging. Of the 15 females taken in the traps over the winter period, nine were not found in any of the burrows. Of these nine, however, one (skunk no. 1) had repeated five times (in 1½ years) and is almost certain to have been a resident. Of the other eight, three were later caught either in the turkey marsh or in Mid-

[11] A 60-acre area in an adjacent section of land to the northwest. It is owned by Mr. Kellogg, and the sanctuary turkey flock has been kept there—hence the name.

TABLE 4. RESULTS OF SKUNK DEN EXCAVATION; 1937

No.	Date (1937)	Locality	Situation	Skunks Found			Remarks
				♂	♀	Total	
1	1/12	Kellogg Farm..	Hillside in field.....	1	10	11	Burrow at least a year old
2	1/22	"	Bank of wash.....	0	0	0	Old burrow
3	1/22	"	Edge of wash.....	1	0	1	Male from burrow no. 1, 1/12/37
4	1/18	"	Side of ditch bank...	1	10	11	Two skunks previously handled in traps
5	1/28	"	Open grassland.....	0	0	0	Old burrow
6	2/ 3	"	Sweet clover field....	0	0	0	Old burrow
7	1/29	"	Under brush heap...	0	0	0	Old burrow
8	2/10	"	Island in swale.....	0	0	0	Fresh tracks leading in and out
9	2/10	"	Grassy hillside.....	0	6	6	All from burrow no. 4
10	2/11	"	Sweet clover field....	0	0	0	Tracks and fresh nesting material
11	2/12	"	Ditch bank.....	0	0	0	Tracks leading in and out
12	2/15	"	Lowland brush.....	1	0	1	Tracks leading in and out
13	2/12	"	Lowland brush.....	0	0	0	Tracks plentiful
14	2/12	"	Lowland brush.....	0	4	4	All from burrow no. 4
15	2/15	"	Base of tree.....	2	0	2	A male opossum also in burrow. 1♂ skunk from burrow no. 4
16	2/16	Turkey Marsh.	Upland woods.....	0	0	0	Old burrow
17	2/16	"	"	1	0	1	Male from burrows no. 4 and 15
18	2/17	Kellogg Farm..	"	0	0	0	Very large nest of leaves; rabbit remains
19	2/18	"	Base of willow tree..	0	0	0	Old burrow
20	2/18	"	Lowland brush.....	0	0	0	Old burrow; tracks
21	2/19	Duck Lake....	Upland woods.....	0	0	0	Tracks numerous
22	2/19	"	Lowland brush.....	0	0	0	Skunk had been followed into this burrow two days previously
23	2/25	"	"	1	7	8	None handled before
24	3/ 3	Kellogg Farm..	Upland woods.....	0	1	1	Not previously handled
25	3/ 3	Turkey Marsh.	"	1	1	2	Female skunk had been marked on K. F. 1/28/37 and retaken there 2/22/37
26	3/ 4	Augusta Creek.	"	0	0	0	Skunk and opossum tracks

land Park and were probably non-residents. The remaining five skunks were taken only once, and there is a good chance that these also were non-residents.

Thus of a total of 62 skunks handled there were 23 females that good evidence indicates were residents (22 from burrows and 1 from traps). Since the work indicates an actual sex ratio of 0.5, one may probably assume an equal number of the males as residents. Thus on a basis of available evidence, the winter population of the 500 acres studied was about 46 skunks.

Evaluation of Data.—The work during the season of 1936-37 appears to be a much better population study than that of the winter before. In 1935-36 the severe weather rendered more skunks inactive, and as calculations were based on trap returns, the figures are probably low. Neither is it known what proportion of the calculated minimum of 40 skunks that used the area were actually resident skunks. It appears probable that, at least in this region, an intensive job of digging is the best method of censusing resident animals.

In terms of the winter census of 1936-37 the Kellogg Farm supported a resident population of one skunk per 10.4 acres of land. What the actual annual yield of fur would be, if the optimum number of animals were harvested, is not indicated. However, as the species is probably polygamous and as ordinary trapping in the winter when most females are holed up takes

many more males than females (Cuyler, 1924),[12] the annual fur crop probably does not inhibit the reproductive potentialities of the population so much as might be expected.

In the literature I have found relatively few estimates of population numbers for skunks. Seton (1909) states, "In the dry part of the pond and poplar belt of Manitoba, it would be safe to estimate the skunk at 1 to every square mile. In the prairie region, it is probably a fifth as numerous, and in the pine forest the number may be again divided by five." It is evident that the status of the Hudsonian skunk in Manitoba is much different from that of the Eastern skunk in Michigan. Of the latter species Norman A. Wood (1922) relates that at his home in Lodi Township, Washtenaw County, about 1870, more than 30 skunks were taken in one trap under an old barn. This sounds much more like the conditions found at the Kellogg Farm.

Bennitt and Nagel (1937) have calculated the skunk population of the state of Missouri for the winter season 1934-35. They considered the average litter to number six; thus the breeding potential of the females is 1:6. However, the most common number of young seen with an adult in the fall is four, giving an actual survival ratio of 1:4. The total kill by man for the year in question was 202,747. The mortality from natural causes was considered as one-third of the harvest by man. Hence the total mortality was near 270,000. On a basis of the above ratio of four young to one female, and considering the sex ratio in the "breeding reserve" to be 0.5, the spring population would be about 135,000 skunks. Since a decline in population was noticed, the authors believe that the actual size of this population was nearer 130,000 animals. These authors also drew attention to the fact that, in making such calculations, a pressing need is felt for more accurate information on the lives of animals. The values given to the necessary assumptions in such a census are no better than the facts at hand, and in our present state of enlightenment, a fairly large error is in some cases to be expected.

If the disproportionately large number of males taken in the trapping season in Texas as shown by Cuyler (1924), in New York as shown by Hamilton (1937a), and in Michigan as shown by the present work, holds good for Missouri, the sex ratio in the spring would not be 0.5, as assumed by Bennitt and Nagel. Hence if fewer males were present, and the animals are polygamous, the spring breeding population would be lower than that computed by these authors.

Ringneck Pheasant

According to local reports the region around the Kellogg Farm has never supported a large population of pheasants. In Michigan in general the pheasant appears to be most common on land that is more level and fertile than this farm. Pheasants have not been hunted on this area since it became a sanc-

[12] I am told by Mr. William Parks, fur buyer at Augusta, that not more than one-fifth of the skunks that he receives in late fall and winter are females.

tuary in 1927, and in the summer of 1933 the Department of Conservation liberated 150 birds as a test planting.

Technique.—Leopold (1931) has said, "It is more difficult to make a census of pheasants than of any other American species." From experiences here this view is entirely concurred in. The regular routine field work over the entire area gave a fairly consistent indication of the number of birds present. However, at intervals when men and dogs were available, the entire farm was covered in an effort to check all parts as simultaneously as possible.

During this study it was not found feasible to census pheasants before October on account of the height of herbaceous cover during summer and early fall. Even in October this difficulty was important, efficiency being higher in November and December. In this work an effort was made to traverse every part of the farm in one day. In several cases, however, a small portion had to be finished on the following morning. In these censuses men were lined up and spaced according to the density of the cover. Dogs were worked at intervals in front of the line of men. In open fields with snow on the ground the sphere of efficiency of a man and a dog was large. However, where even low cover was present a man was of little use, and the dependence was almost entirely on the dog (see also Wight, 1931). On several occasions it has been possible to stand quietly outside an area of brush and to see a pheasant double back and escape a dog without flushing. Even these animals do not put up every bird. A repetition of censuses was found to be necessary if accurate information on the number of pheasants present was to be obtained. There has been frequent interchange of birds with surrounding areas that very materially altered population numbers.

Daily field work on the farm has also revealed movements from or to the area and served to show population trends. In addition, box traps took pheasants fairly regularly, and the number of individuals trapped in the winter season was a significant index.

From the standpoint of a pheasant study the wire box traps used are not to be recommended. Birds in traps easily become frightened and almost invariably skin the top of the head while the traps are being approached. In this work pheasants have been taken in box traps 73 times and 7 mortalities have resulted from injuries so received. Wire funnel traps were experimented with but were found to be relatively inefficient as used here. A cat and a Cooper hawk caused the death of three birds in such traps. All but three mortalities due to technique were replaced by liberating birds of similar sex reared at the state game farm.

Pheasants were marked with leg bands and, during the second winter, tails were bobbed to a length of about 6 inches. This did not appear to impair the flying ability of the birds. Such bob-tailed pheasants were easily recognized in the field, although individuals were not indicated.

Population in Fall, 1935.—In 1935 the area was censused on October 14,

October 30, and December 20. The first two censuses were taken under conditions of high ground cover and only 400 acres were worked. Dogs could not at this time be used on the sanctuary. In the first census 29 pheasants were flushed, of which 14 were cocks and 15 were hens. In the second, which was relatively inefficient due to a lack of help, 20 pheasants were flushed of which 10 were cocks and 10 were hens. The census of December 20 was taken under more favorable conditions, the whole area was covered, and 28 pheasants were found. In the latter tally 14 were cocks, 13 were hens, and 1 was unknown. In this census it was felt that a fairly accurate approximation of the number of birds on the area was made. All indications point to an October population of between 30 and 35 pheasants on this 500 acres. Evidently the sex ratio was perfect. By December 20 the number was probably very close to the figure of 28 obtained in the census.

Field work showed that pheasants were well distributed over the farm during this period. At least four birds were known to be using the turkey marsh and the farm. In early fall hayfields and open areas were being much used, but by late December pheasants were most often found in thick brush or conifers. As an index to the late fall population the figure 30 may be taken as a reliable estimate. During the fall and winter 20 pheasants were taken in the box traps and banded. There were five recorded mortalities among unbanded birds. Hence, by this method 25 individuals were accounted for.

Population in Spring, 1936.—A census of the area on March 23 produced 20 pheasants, 6 of which were cocks, 13 were hens, and 1 was unknown. In April the localization of cocks on particular territories, as well as their crowing, made a check on the number of birds comparatively easy. It is fairly certain that there were about 12 hens on the area at this time and from 9 to 12 cocks. Of the latter only 4 or 5, as judged by their regular association with hens, appeared to be mated. During the winter 25 individual pheasants were handled. Five of these were mortalities, leaving 20 birds theoretically alive. Some of the latter may, of course, have left the area and others moved on. Only four broods are known to have been reared on this area and aggregated about 35 young pheasants in June.

Population in Fall, 1936.—A census on October 9, 1936 covering the farm (400 acres) but not the sanctuary showed a total of 22 birds flushed. Eight of these were hens, 13 were cocks, and one was questionable. At least a few pheasants were known to be on the sanctuary, which could not be worked with dogs due to the presence of migrant waterfowl. Evidently the fall population in 1936 was much the same as in 1935.

In December pheasants became fewer in number and by mid-January birds were seldom seen on this area. The pheasants from the farm had, for the most part, moved north and gathered in a large thicket of lowland brush southwest of Duck Lake. This covert lies just across the road from the northeast corner of the Kellogg Farm. Chicken house litter containing

cracked corn was being spread on the corner field of the farm and these pheasants at times fed here in a flock. The largest number counted was 24, but a flock of 15 to 18 was common. A census was taken on January 22 when this flock was absent. Only five pheasants (four cocks, one hen) were found. Few observations were made during the spring, but breeding birds were again back on the area.

Summary.—The number of pheasants present on the Kellogg Farm was indicated by censuses taken with men and bird dogs, by regular field work, and by birds taken in box traps. In late fall of 1935 the population was about 30 pheasants, with the sexes equal in number. The population density was about one pheasant to 16.6 acres. In the following spring the breeding population numbered about two dozen birds. In the fall of 1936 the population appeared to be much the same as in the year before. In winter, however, most of the birds of this area moved north into the next section, so that a census in January indicated only about five pheasants on the farm.

Quail

Quail populations in this portion of the state appear to be variable over small areas and short periods of time. The bird is not hunted as game in Michigan and hence its protection on the Kellogg Farm does not render the area exceptional in this respect.

Technique.—The quail population of this area was inventoried at the same time as were the pheasants; hence the same methods were used. As quail were in coveys during fall and winter, however, numbers could be fairly well checked merely by locating the coveys present. The principal difficulty was that during the winter quail were often in thick brush and had to be flushed to be counted. Accurate counts could, under these conditions, not always be made. In addition, the regular flushing of the birds disturbed them and evidently served to break up coveys. Catching a portion of a covey in a trap also tended to separate the birds. The interchange of quail between the different groups appeared to be frequent. In this connection Errington and Hamerstrom (1936) point out that they have made it a general policy not to do much banding or collecting on the areas where populations were to be observed under conditions as natural as possible. In some cases coveys could be checked by track counts without molesting the birds, but these occasions were relatively infrequent. In general, it may be said that work on this project appeared to disturb quail more than any other species that was studied.

Population in Fall, 1935.—In the first fall census (October 14) two coveys of 17 and 7 each were found. In the second of these five of the birds were seen to be juvenals. On October 30 three coveys were on the area and numbered 18, 17, and 5 quail respectively. One covey evidently moved onto the farm late in October. That daily field work was more reliable than infrequent inventories is shown by the results of the December census. At the

time of this inventory only 23 quail could be found. Yet during much of early December, field work showed that four coveys aggregating 42 birds were present. A bevy of 14 shifted onto and off the farm several times.

When snows became deep during January and February it was very difficult to follow the movements of the coveys. Birds shifted, ranges overlapped, and groups appeared to split and re-combine. It is doubtful whether by any method an accurate check could have been kept on these quail. A brief summary of observations will indicate the type of activity that occurred.

In January a covey of 14 that had been on the south side of the area (in December) disappeared as residents. They evidently moved south but reappeared from time to time, and 10 of the birds were trapped and banded. Half a mile south a woman began feeding from 15 to 20 quail and it is possible that some of these may have been all or a part of the covey of 14. On the north side of the farm a December covey of 15 also moved off the area, and soon after, 18 birds were seen north of the road feeding with a cock pheasant in a patch of corn. As three birds had also been flushed at times, it is possible that the 18 represented these plus the covey of 15. This is largely supposition, however, as the three may have moved south on the farm and joined other birds. A group of 10 quail near the middle of the area in December remained near a feeding station in January and were local in range but not always constant in numbers. Several times five or six birds flushed instead of the usual number. In February a covey of 15 quail appeared on the southwest side of the sanctuary and were fed there in a swale.

The nearest that I can come to tracing the history of a covey is one that was almost undisturbed in an experimental food patch in the turkey marsh. In February hemp projected above the snow and was fed upon by these quail, which roosted in the open. On February 11 there were 12 birds. Three days later there were still 12, but by the last of February the number had decreased to nine. On March 18 and 20 only six birds were flushed. Evidently the covey was breaking up at this time.

From the above discussion it is evident that any fixation of a population figure for this area in fall or winter would be somewhat arbitrary. The maximum population appears to have been 42, although shifts altered this considerably.

Population in Fall, 1936.—In late summer of 1936 it appeared that two broods that had been reared on the farm joined to form a covey of 25. In September these quail moved north into the turkey marsh and did not return to the farm area. During the fall and winter only 10 quail were present and these at times evidently moved into the next section to the north. The maximum population for the second fall season thus was 10. At times no birds at all were present, although there were bevies to the south and to the north on other areas.

There is little indication of the actual numbers on the area in spring. In

1935, 1936, and in 1937 quail were well distributed over the farm, and pairs were seen frequently. During the spring of 1936 as many as five calling males could sometimes be located almost simultaneously.

Summary.—The activity of quail has been characterized by frequent movements onto and off the area; thus populations have fluctuated radically. Evidently the maximum number of bobwhites that have been on the farm in two years is 42—the number present in early December, 1935. In late fall and winter of 1936-37 the maximum number of quail found was 10 and at times none at all was on the farm. On such a small area as this it is difficult to assign a numerical value to the quail population, due to the frequent changes resulting from the movements of coveys.

Species of Lesser Abundance

The New York weasel appears to be present in relatively small numbers throughout most of its range (Audubon and Bachman, 1849). Seton (1929) estimates its maximum numbers as a pair to the square mile during primitive times in Manitoba. From bounty records, he computes a population of about five to the square mile in Pennsylvania. The largest concentration of weasels that I have found recorded is indicated by Miner (1923), who took 57 of these animals in three traps during one summer. Tracks in winter were the best indication of weasel abundance on the area studied. On a basis of such evidence the weasel population of the Kellogg Farm was about half a dozen animals in January, 1937. Tracks were centered around such locations as a Microtus colony on the south side, the sanctuary woods, a buttonbush swale near the center of the farm, and the oak-hickory brush on the north side. Three weasels were taken in box traps during late winter. All of the animals handled were males.

The house cat has been one of the most consistent animals on the area from the standpoint of numbers and activity. In all kinds of weather cats have been found active, and whenever tracking conditions were good, field work indicated that from one to five animals had visited the area. During the first year of this work 30 individual cats were caught in the traps. Inasmuch as many of the animals taken were probably pets, they were kept for two days, in case they were called for. Of the 30 taken 23 were not claimed and were killed. During the second winter all that were caught were killed immediately and the stomachs preserved. Twelve cats were taken from September, 1936 to April, 1937. Evidently some of the animals found on the farm were abandoned by summer residents in Midland Park, and "drift" from other localities probably replenished the population here, much as on several areas cited by Leopold (1931). Only one case of breeding here is known, a female having borne a litter in one of the sanctuary buildings. The average number of cats on the farm at night was probably three or four.

The opossum has within the past 20 years extended its range northward into Michigan (Seton, 1929). At the Kellogg Farm it is not now abundant, opossums having been taken in traps only 30 times during the two winters of the work. Twelve individuals were marked by toe clipping. Three of these animals were juvenals taken in the fall of 1936. In the total of marked animals six were males and six were females. There is little to indicate the number of animals usually present, though from tracks and trap records in winter it probably was not more than three or four.

In summer raccoon tracks have frequently been observed in the swales on the sanctuary. Two of these animals were seen at dusk on an evening in October, 1934, and one (a female) was captured in a box trap in April, 1936. In accordance with the sanctuary policy it was necessary to deport the latter animal and liberate it elsewhere. There are several more sight records of raccoons and all were obtained in summer. No tracks have been seen after October, and the species was undoubtedly absent during the winter. Probably not more than two or three have been present at any one time in summer.

There is only one record of a red fox on the Kellogg Farm in two years. In January, 1937 tracks of one of these animals were present for several days and a fox was reported seen in the next section to the north. No other signs of the species have been found.

Woodchucks are not common on the area at present, although reports indicate that they were when the farm was established. Old burrows are very numerous, and doubtless many were originally dug by this species, although they are now used by skunks. Woodchucks have been seen only three times in three years. In addition, two specimens were caught in steel traps in the farm woods in the spring of 1937.

On one occasion (January, 1936) during the day two great horned owls were located almost simultaneously in the farm woods. Two birds have rarely been heard calling, but more than this are not known to have been present at one time. It may safely be said that ordinarily not more than one horned owl was on the area. Although regularly observed only in winter, the species was present intermittently in summer. In June, 1936 one of these owls was caught in a chicken coop a mile south. In June, 1937 young chickens were disappearing from the poultry yard on the Kellogg Farm. Steel traps were set and two horned owls were caught.

During the winter of 1935-36 from one to three Cooper hawks were regularly to be found on the farm. In the following winter the number was larger, appearing to vary from two to five. During the latter season three or four hawks could frequently be seen in the course of a day's field work. The difference in size between the sexes and in color between adults and juvenals often made it possible to count individuals with little chance for error. Most of the hawks seen on this area, however, have been juvenal females.

SMALL MAMMALS

Of the two species of ground squirrels on the area the thirteen-lined spermophile is by far the most abundant. Although their burrows are not found on cultivated ground, these rodents inhabit every grassy fence row and all the meadows and permanent hayfields, as well as the open areas on the sanctuary. No attempt has been made to compute the numbers of the species. It is sufficient to say that it is the most abundant mammal on the area larger than a mouse and that it is very commonly seen wherever there is open grassland.

The chipmunk is most plentiful in the farm woods, although nowhere does it reach the apparent population density of the foregoing species. In the spring of 1936 one pair inhabited the sanctuary woods. There appear to have been never more than two or three pairs on the entire sanctuary during this work. The species probably is not of great ecological importance on the area.

Flying squirrels were very infrequently seen during this study. Two were taken in steel traps in the turkey marsh and one was found dead in a box trap in the farm woods. Flying squirrels were observed in this woods on two occasions. Their strictly nocturnal habit makes observation difficult, although it is safe to say that they have been relatively uncommon on the area discussed.

Two species of mice are the most abundant mammals on the farm. In the fall and winter of 1935-36 both the prairie deer mouse and the meadow vole were very numerous. In long grass, thick alfalfa, or sweet clover, meadow mice were common, and many of their globular grass nests were found above ground. On the other hand, all of the open grass areas, hayfields, and even cultivated fields were occupied by the prairie deer mouse, so that for the area as a whole the latter species was very probably most plentiful. The dry summer of 1936 appeared to affect the field mice adversely. The population quite evidently was smaller in the following fall and winter than in the season previous. Many of the old colonies were entirely deserted. Numerous traps could be set in such places without taking an animal. A few colonies on the area, however, appeared to be as populous as ever. The drop in numbers seemed to be correlated with the drying up and comparative barrenness of localities that had supported a lush growth of grass or clover during 1935. There was no apparent diminution in the numbers of the prairie deer mouse, and in the second winter there is little question that the latter species was the most numerous mammal on the area.

The white-footed mouse was the most common small mammal in brush and woodland. The two species just discussed, with the addition of this mouse, form the bulk of the small mammal "key industry"[13] on the area. The woodland mouse, owing to its more restricted habitat, was not so abundant

[13] See page 400.

here as the prairie deer mouse or the meadow vole; although it was sufficiently numerous to be an important quantity in the food cycle.

The short-tailed shrew may, from its abundance, be added to the three species listed above as an important prey animal on this area. During the dry summer of 1936 it was common in the farm woods, though none could be taken in fields adjoining. In the following winter few were found in the woods, but the species was numerous in lowland brush. It was also taken in marsh grass on numerous occasions in winter. The very dry summer of 1936 apparently restricted this animal to low ground and woodland and may have reduced its numbers. Enough data are not at hand, however, to demonstrate this point.

The prairie mole was very plentiful during this study and probably of considerable ecological significance. Its tunnels were found on lawns, in pine plantings, and in grassland everywhere.

Only four individuals of the Cooper lemming-vole were trapped on the Kellogg Farm, and the species may be listed as very infrequent. Only two specimens of the pine mouse were taken, both of which were in the basement of the residence at the sanctuary. Jumping mice were caught on a few occasions in box traps, but less than a dozen individuals were caught or seen in three years. These three rodents are probably of little significance bionomically.

Masked shrews were not common on the area. Several were caught in mouse traps or found dead. Only one least shrew was taken. The star-nosed mole was not recorded during this study, but a specimen was captured on the sanctuary in 1933.

In summary, at the time of this investigation the most abundant small mammals, which form the small mammal key industry on the Kellogg Farm, were the thirteen-lined spermophile, prairie mole, prairie deer mouse, meadow mouse, white-footed mouse, and short-tailed shrew.

ANIMAL INTERRELATIONS

The purpose of the following discussion is to picture, insofar as possible with the data at hand, the mosaic of interrelationships that constitutes the life pattern of this area. Species are here considered chiefly from a qualitative standpoint, although little space is given to those that are not of sufficient size or present in sufficient numbers materially to affect the other animal populations. The more abundant upland mammals and birds, which characterize the area, are dealt with most completely in this section, as in the foregoing discussion of populations.

In treating the mutual effects of one animal species on another it appears most convenient to separate the subject into three major divisions. Animals are first considered from the standpoint of where they live. Species associated in the same habitats will obviously be most capable of close interaction. Time

of activity is taken as another point of emphasis. In the area studied the Cooper hawk is probably of little importance to the Virginia rail, as the former, although eminently raptorial in habit, is present only in winter; while the latter, definitely a prey species, is here only in summer. As another example, the screech owl probably seldom feeds upon the thirteen-lined spermophile, as the owl is nocturnal and the ground squirrel is exclusively diurnal. The third consideration has to do with the food habits of animals. This is, doubtless, the most vital relationship of all. It may be considered from two standpoints: animals of similar habit that compete for food; and the relations of carnivores to the species upon which they prey. Few species have been studied completely enough in this work to indicate many of the food relations occurring here. Hence the work of others is used wherever it is of significance. In general, what has been found true of a species on other areas can, if properly used, apply here. Such a method is considered definitely a part of this type of ecological research.

Habitat Relationships

If an attempt were made to describe transition zones and seasons, this discussion could well become unmanageable. Hence clearly defined types are chosen for analysis, with the understanding that a great variety of intergrading conditions exists. Habitats are arbitrarily grouped for discussion wherever on this area a similarity of use by animals appears to justify it.

Animals Associated in Summer Habitats

In most cases of common resident species certain habitat preferences have been manifest. The New York weasel is an exception to this. These animals or their signs were found in several types of habitat in summer, although observations were not numerous. Weasels in general have been observed in various situations (Burroughs, 1900; Nelson, 1918; Bailey, 1926; Leopold, 1937) and it is doubtful whether there is much of a summer habitat discrimination in this species. The animal is considered here to be a potential inhabitant of any of the following cover types and is not discussed under the separate headings.

Swales and Lowland Brush.—In the summers of 1935 and 1936 raccoon signs were common in the swales and around the margin of Wintergreen Lake. On one occasion two animals were seen together. Muskrats were always present in numbers during the summer season. These two species are the mammals most typical of this habitat, although in brush along swales the meadow jumping mouse was often found. The bird life was more varied. The great blue heron, little green heron, and the marsh hawk were regularly present, the least bittern, American bittern, and Florida gallinule occasional, the sora and Virginia rails frequent, and the mallard duck common. The most typical inhabitant of swales is the redwing blackbird. In and around the brushy margins yellow warblers, goldfinches, and song sparrows nested

commonly; and the catbird, brown thrasher, alder flycatcher, and kingbird were frequently seen. Pheasants (particularly cocks) were often found in lowland brush at this season.

Fields and Grassland.—The common summer mammals of this habitat are the skunk, house cat, cottontail rabbit, thirteen-lined spermophile, prairie mole, and prairie deer mouse. Woodchucks were present on the Kellogg Farm though not numerous. Where grass is deep the deer mouse is replaced by the meadow mouse. Both species have been found in alfalfa fields. The spermophile favors dry, open situations. On plowed ground skunks and the prairie deer mouse were the mammals most often found. The marsh hawk and crow were common over open grassland, and great blue herons not infrequently hunted here. Red-tail hawks often hovered low over the fields. Birds more properly belonging to the habitat in summer, however, are the ringneck pheasant, bobwhite quail, field sparrow, vesper sparrow, grasshopper sparrow, meadowlark, and horned lark. The bobolink, dickcissel, and Henslow sparrow occurred here sparingly at times.

Upland Brush.—In this habitat the skunk, house cat, cottontail rabbit, and white-footed mouse were common. In long grass the field mouse was nearly always present. Some woodchuck dens were also found in upland brush. The birds ordinarily found here were the catbird, brown thrasher, cardinal, goldfinch, mourning dove, chipping sparrow, pheasant, and quail.

The upland coniferous plantings have a well-defined fauna apart from the deciduous type. The cottontail rabbit, the common mole, and the white-footed mouse were nearly always present; and in thick grass the meadow mouse was common. Robins and mourning doves nested abundantly in the conifers, and catbird nests were not infrequent. Pheasants, paricularly cocks, were often seen here in summer. The small spruces and junipers were especially favored by the chipping sparrow, which nested regularly in this type of cover.

Woods.—The summer population of the upland woods is typified by the fox squirrel, flying squirrel, chipmunk, white-footed mouse, and short-tailed shrew. The latter species showed an especial preference for this habitat during the very dry season of 1936. Woodchuck dens were common here, but skunks appeared to be only occasional in summer. Rabbits also were relatively infrequent. The avifauna is characterized by the crow, red-tailed hawk, red-headed woodpecker, flicker, great crested flycatcher, wood pewee, red-eyed vireo, warbling vireo, Baltimore oriole, and blue jay. So little lowland wood being present, it is not characterized by a well-defined fauna on this area. It has been noted, however, that several opossum dens were in this type of habitat.

Animals Associated in Winter Habitats

Fields and Grasslands.—One of the most typical inhabitants of this type of territory is the prairie deer mouse. In situations having a dense growth

of Kentucky bluegrass, alfalfa, or sweet clover, winter colonies of the meadow mouse have often been present. Under deep snow, however, Microtus colonies have been observed to move into upland brush or coniferous plantations where they were not present in summer nor in winter when snow was absent. Weasels were frequently found around mouse colonies, short-tailed shrews have been taken in the runways, and skunks were at times active here during periods of mild weather. The prairie mole is most typically found in grassland. House cats hunted this habitat under all conditions. In the winter of deep snow (1935-36) flocks of from 10 to 100 tree sparrows and juncos, with a few song sparrows, were common in the open fields. Horned larks, in flocks of a dozen or so, were also present. In February, when the snow reached a depth of one and one-half feet the flocks began to disappear until, late in that month, few of these birds were to be found on the area. In the mild winter of 1936-37 there was little snow until March. The songbird flocks of the preceding winter were conspicuously absent. At times hardly half a dozen tree sparrows and juncos were to be found, and horned larks did not arrive until mid-February. Quail and pheasants have been found in the open under many conditions, though most often when snow was not deep. When snow was absent, pheasants regularly fed in the fields. Crows were active in this habitat regardless of conditions.

Swales.—When swales were frozen, the marsh type of cover was used by cottontail rabbits, meadow mice, prairie deer mice, short-tailed shrews, and masked shrews. The most typical mammalian inhabitant is, of course, the muskrat. The marsh grass and cat-tail have also served as cover for pheasants and quail upon occasion. Nearly all of the songbird species listed for grassland have used the marsh in much the same manner.

Brush.—In winter lowland brush functions much the same as upland brush for most species. The muskrat, however, is more common in and around the lowland brush areas, and the short-tailed shrew has been found in greatest numbers in such situations. Both upland and lowland types are extensively used by the cottontail, weasel, skunk, house cat, and white-footed mouse. Pheasants and quail are very dependent upon brush cover in winter, and the Cooper hawk was most often found in such areas. Among smaller birds the cardinal, blue jay, chickadee, downy woodpecker, song sparrow, junco, and tree sparrow were common. Conifers were most favored by rabbits and pheasants as winter cover. The Cooper lemming mouse was taken several times in conifers and also in upland brush.

Woods.—The fox squirrel is most typical of this habitat in winter. Skunks, house cats, weasels, rabbits, and white-footed mice are the other mammals that have been found here. Among birds the crow, great horned owl, and Cooper hawk were winter inhabitants, as were the white-breasted nuthatch, chickadee, and downy woodpecker.

Use of Dens

Old woodchuck dens were numerous, although only a few woodchucks were to be found on the Kellogg Farm during this study. Skunks use practically any kind of burrow, including woodchuck dens, as well as those dug by themselves (Nelson, 1918; Seton, 1929; Johnson, 1930; Goodwin, 1935). Such holes undoubtedly form important winter cover for rabbits (Trippensee, 1934; Tubbs, 1936). Rabbit tracks have frequently been seen leading into burrows which skunks were known to have used at some previous time. When water was low in winter they also occupied old muskrat burrows. Weasel tracks and tracks of the white-footed mouse have been found which indicated a use of such dens. One skunk den that was excavated contained two skunks and an opossum.

Dens may be considered to affect the interrelations of animals in two principal ways. The construction of burrows by the woodchuck and the skunk may abet the efforts of a rabbit to escape from enemies above ground and contribute to its comfort during severe weather (Leopold, 1931; Trippensee, 1934). These same burrows, however, may serve the weasel and skunk in enabling them more easily to catch the rabbit (Audubon and Bachman, 1849; Kennicott, 1858; Stone and Cram, 1920). The weasel in particular uses its small size and sinuous body to good advantage in entering the burrows of small animals. Bailey (1926) states that on the plains it regularly enters the burrows of pocket gophers. Audubon and Bachman (1849) and Seton (1929) refer to its pursuit of mice and ground squirrels into their homes. Kennicott (1857) and Cory (1912) speak of weasel nests in "deserted" ground squirrel burrows. During this study weasel tracks were very frequent around winter colonies of Microtus. In the tunnels under deep snow these animals were probably protected from most other enemies. A weasel has been seen dodging in and out of the burrow of a mouse, and its stomach was found to contain the remains of the burrow's probable owner (*Peromyscus* sp.). A vivid impression remains that this animal is primarily adapted to hunting in small holes. Such burrows, coupled with the weasel's capacity for overindulgence in the matter of killing (De Kay, 1842; Coues, 1877; Merriam, 1886; Lantz, 1923), appear to make it possible for a small number of weasels to be a material factor in the lives of a very large number of Microtines and other Rodentia.

Activity Relationships

As elsewhere pointed out, animals are brought into most direct contact with one another, first, by being in the same habitat; and secondly, by being active at the same time. This is not, by any means, the only way that species interact; but it is the principal way in which predator-prey food relationships are brought about. As a consequence, it is considered important in this discussion.

Seasonal Activity

Certain species which are undeniably important as bionomic factors on this area are of seasonal occurrence only. An animal may be designated a seasonal either because it is present and dormant, or absent through migration. Predominants are present and active through the year.

Predominant Animals.—The carnivorous mammals which are regularly present and perennially active on this area are the house cat, weasel, opossum,[14] prairie mole, short-tailed shrew, and masked shrew. The winter activity of the mole has been questioned, but the animal is now known to be active throughout the year (Scheffer, 1927; Gregory, 1936). Fresh workings during the winter have often been seen in the course of this study, and on January 10, 1936 a specimen was found above ground burrowing about through an inch of snow.

Among the herbivores the cottontail, fox squirrel, muskrat, prairie deer mouse, white-footed mouse, Cooper lemming-vole, and meadow mouse are predominants. In this work no flying squirrel records have been obtained in winter. The consensus of opinion, however, is that the animal does not hibernate (Kennicott, 1856; Anthony, 1928; Gregory, 1936), although it is believed to be inactive and to remain in the nest during very cold weather (Merriam, 1886; Wood, 1910; Nelson, 1918; Stoner, 1918; Stone and Cram, 1920). In this case it may be listed as predominant.

Predominant birds on this area are the pheasant, quail, screech owl, crow, mourning dove, flicker, hairy woodpecker, downy woodpecker, blue jay, chickadee, starling, English sparrow, goldfinch, and song sparrow. The great horned owl is a regular winter inhabitant but is, apparently, only occasional here in summer; hence it is not included in the above. The goldfinch and song sparrow have been present in winter in small numbers only. The horned lark was present throughout the winter of 1935-36 but did not arrive until February in 1937. It is ordinarily not predominant, but a late winter and summer resident.

Seasonal Animals.—The annual migration of most birds and the winter dormancy of certain mammals give the winter and summer vertebrate populations of the Kellogg Farm materially different aspects.

Species that are dormant in the winter are the woodchuck, spermophile, chipmunk, jumping mouse, and the skunk. Skunks do not hibernate, as do the other species, but remain inactive in dens during the coldest part of the winter. A thaw will find some old males abroad, but during January and February the number of active skunks is small.

Of the migratory birds that visit the area a few species are present only in winter. Such residents that leave in spring are the Cooper hawk, great horned owl (with exceptions), tree sparrow, and junco. Snow buntings, redpolls, and siskins are only occasional.

[14] Opossums have, however, been inactive during very cold weather.

With regard to summer populations, all of the mammals listed as predominant or dormant in winter are, of course, active in summer. One species, the raccoon, has been found on the area only in summer. At this season a few individuals intermittently fed in the swales. No raccoon signs were found in winter or spring. Evidently these animals had their dens on some near-by area.

Most bird migrants are found in this locality only in summer. The following species were regularly present during three seasons: pied-billed grebe, great blue heron, little green heron, black-crowned night heron, American bittern, least bittern, Canada goose, mallard duck, red-tailed hawk, marsh hawk, Virginia rail, sora rail, coot, killdeer, spotted sandpiper, herring gull, ring-billed gull, black tern, black-billed cuckoo, nighthawk, chimney swift, hummingbird, kingfisher, red-headed woodpecker, kingbird, great crested flycatcher, phoebe, alder flycatcher, least flycatcher, wood pewee, prairie horned lark, tree swallow, bank swallow, rough-winged swallow, barn swallow, purple martin, house wren, catbird, brown thrasher, robin, bluebird, starling, red-eyed vireo, warbling vireo, yellow warbler, meadowlark, redwing, Baltimore oriole, bronzed grackle, cowbird, towhee, grasshopper sparrow, vesper sparrow, chipping sparrow, and field sparrow.

Species in the check-list (see appendix) that are not discussed here as to seasonal activity either have occurred sporadically or have been recorded only during the spring and fall migration seasons.

Daily Activity

Among the predominant animals of the Kellogg Farm the following are chiefly nocturnal: house cat, opossum, rabbit, muskrat, prairie deer mouse, white footed mouse, and flying squirrel. The last three named appear to be exclusively nocturnal. All the others have been seen abroad in the daytime. From records secured in this work weasels appear to be active at any time through the day or night. This is in agreement with the findings of Coues (1877), Herrick (1892), and Nelson (1918). Kennicott (1857) considered weasels to be principally nocturnal. As for the short-tailed shrew, few records of daytime activity have been obtained here, but Nelson considers it to be active with little regard to the time of day, and Williams (1936) found it active both day and night. All other of the perennially active mammals are diurnal.[15] Of the birds listed as predominant the screech owl is the only nocturnal species. All others are diurnal.

Of the species present in summer the skunk is for the most part nocturnal, though individuals have been seen at various hours throughout the day. Raccoons are doubtless nocturnal, although one morning observation was made. The jumping mouse has been seen several times in the daytime, although the species is nocturnal (Kennicott, 1856; Seton, 1909; Nelson, 1918). The

[15] Few data have been obtained here regarding the activity of meadow mice, but Hamilton (1937b) found them to be chiefly diurnal with activity greatest in early morning and late afternoon.

woodchuck, spermophile, and chipmunk are diurnal. Other mammals active in summer have already been discussed. Of the summer birds the screech owl has been cited as nocturnal. The night heron is crepuscular and nocturnal. The great blue heron is active both day and night, as is the nighthawk. Intensive study has not been made of the marsh and shore birds, though most are active by day and, except during migration, appear to be relatively inactive at night. Nearly all the smaller birds are diurnal.

Most of the winter birds and mammals have been referred to under predominants. Of the seasonal species the great horned owl is nocturnal and the tree sparrow and junco diurnal.

Food Relationships

Plant and animal populations are most effectively unified into ecological communities through the absolute necessity of each individual in every species for food. Considering the patently fundamental place of plants and invertebrates in the food relationships of animal society, a discussion of birds and mammals alone necessitates a somewhat artificial simplification. No attempt is made here to treat even the latter groups completely. Certain phases of the subject have been investigated which appeared to be important to the status of one or several of the more influential species, and which seemed to be amenable to logical analysis under the existing conditions.

Elton (1927) resolves the food relations of animals into four principles which he designates as follows: (1) food chains and the food cycle, (2) size of food, (3) niches, and (4) the pyramid of numbers. It will be profitable to review the implications of each of these principles.

Herbivores are the fundamental class in animal society, and through them the energy derived by plants from sunlight is transferred to all the carnivores. Food habits among carnivores differ widely, certain species being preyed upon by certain other species, which may in turn be eaten by still larger forms. Thus chains of animals are formed, linked together by food. These may extend from the smallest herbivores up to the largest carnivores which dominate the community. The aggregate of all the food chains in a community is spoken of as a food cycle. As each species in a food chain is usually larger than the species below it, the principle of size of food is introduced. Animals utilize food within certain size limits because species above these limits are too large to be killed and species below are too small for the numbers that can be eaten. Thus an animal occupies a specific place in a community because it utilizes food of a certain size. The plan of communities everywhere is much the same, and although species of similar habit in widely separated communities may differ in taxonomic position, their functions or "niches" in the ecological structure may be essentially the same. One well-defined niche is that of herbivorous animals that are so numerous as to support a large number of carnivores. These herbivores form what is termed a "key industry," a

good illustration of which would be the small mammal key industry that occurs nearly everywhere. It will be observed that, progressing downward in the food chain, one finds that as animals decrease in size they increase in numbers; so that, considered numerically, food relationships can be represented by a pyramid with a multitude of small animals at the base, smaller numbers of animals intermediate in size in the middle, and finally tapering off to a few individuals of large species at the top. Enough data are not available to treat the fauna of the Kellogg Farm completely from all of the angles cited above. These conceptions stated by Elton are considered, however, a fundamental preface to any discussion of food relations, as they create a pictorial structure in which can be placed any apparently disconnected facts which are brought to light.

Food Relations of Herbivores

Inasmuch as herbivorous species do not habitually utilize one another as food, their most apparent food linkage is through competition for a common supply. In summer this rivalry has not appeared to be intense, as the superabundant vegetation present on this area has evidently been more than enough to supply the needs of all. In winter the problem is vital, as food supplies may be used up or become less available through deep snow. The present study treats the winter season only.

Herbage Feeders.—Two species of mammals, rabbit and meadow mouse, are the most influential herbage feeders on this area. The muskrat belongs more properly to the aquatic habitats and was not intensively studied. Animals that feed upon the leaves and stems of plants may not only compete for food but, through the girdling of shrubs and trees, destroy cover that can materially affect future winter populations of both carnivores and herbivores.

Rabbits eat a great variety of herbaceous vegetation (Seton, 1909) and apparently prefer this type of food. In the very open winter of 1936-37 very little bark of any kind was taken. A winter staple on the Kellogg Farm is buckhorn. Under conditions of less than an inch of snow rabbits often scratched through and fed upon this plant.[16] Yarrow is another herb that was so taken, and rabbits have been seen eating dandelion and bluegrass.

Under the conditions of very deep snow existing in the winter of 1935-36 very little herbaceous vegetation was available and, apparently as a consequence, rabbits fed extensively upon bark. These rodents use woody plants as food by pruning, budding, and gnawing the bark from the stems. Kennicott (1857) found that pruning was the type of work most frequently found in orchards. However, on the Kellogg Farm bark feeding was of more frequent occurrence than pruning. Feeding upon woody plants by rabbits has been described by Audubon and Bachman (1849), Lantz (1907a, 1929), Todd (1927), Nelson (1918), Stoner (1918), Trippensee (1934), and Siegler (1937).

[16] Kennicott (1857) states that rabbits seldom, if ever, dig through the snow, and this has usually been found true where its depth was an inch or more.

FIG. 16. Staghorn sumacs barked by rabbits during the winter of 1935-36.

On the area treated here dwarf sumac and staghorn sumac were the two species that were most often taken. Figure 16 shows the "rabbit line" on staghorn sumacs in a kettle hole near the farm. Twenty-eight species of woody plants were observed to be used, among which were willow, sassafras, wild crab apple, buckthorn *(Rhamnus cathartica)*, wild black cherry, elder, rose, grape, and several species of dogwood. Oak and even hickory were eaten in some places. Although the work of rabbits was widespread and easily noticed in winter, it was of little actual significance in reducing cover on the area.

Meadow mice are known to live to a great exent upon grass and other green herbaceous food; but in winter, especially when snow is deep, they eat the bark from nursery stock, shrubs, and trees of many kinds (Kennicott, 1856; Butler, 1892; Herrick, 1892; Bailey, 1900, 1924; Lantz, 1907b; Evermann and Clark, 1911; Cory, 1912; Nelson, 1918). On the Kellogg Farm in the winter of 1935-36 meadow mice extended their range under cover of the deep snow into tree and shrub plantations where they had not been numerous before. After the snow melted, twelve species of trees and shrubs were found to have been girdled by these mice. The most extensive girdling was done on Scotch pine. In the turkey marsh to the northwest of the farm, in a planting of 97 pines only 27 trees escaped damage and about 50 were killed (fig. 17). Other conifers that were taken were western yellow pine, Austrian pine, and ground juniper. In a mixed planting of white, western yellow, and Austrian pines on the farm nearly all of the latter two species were girdled, although white pines were found to be untouched. Deciduous shrubs and

FIG. 17. Scotch pines girdled by meadow mice in the winter of 1935-36. The tree in the right foreground is about 5 inches in diameter.

trees that were preferred by the mice were mulberry (*Morus rubra* and *M. alba*), wafer ash or hoptree (*Ptelea trifoliata*, fig. 18), wild black cherry, honeysuckle (several cultivated species), and catalpa (*Catalpa speciosa*, fig. 19). In a near-by orchard apple trees had the lower limbs barked where they were covered by snow. In the winter of 1936-37 very little bark was taken by mice. This is probably due in part to the fact that field mice were fewer in numbers, but may be ascribed principally to the lack of snow. As a result herbaceous plants were available, and there was no protection for the above-ground activities of the species.

The work of rabbits and meadow mice is not difficult to distinguish. Rabbits leave ragged edges and do not take the bark cleanly, whereas the mice remove it smoothly down to the white wood and completely lay bare the area worked upon. Rabbits eat bark above the level of the snow; and all of the observed mouse girdling has been done in tunnels beneath its surface.

Woody vegetation has been sufficiently abundant on the area studied to obviate the necessity for any intense competition between the rabbit and meadow mouse for this type of food. Meadow mice have done more to reduce

FIG. 18. Wafer ash or hoptree (about 1 inch in diameter) girdled by meadow mice during a period of deep snow.

cover, due to the species attacked, than rabbits; however, all of such rodent activity together has not been sufficiently intensive to affect materially the amount of cover present. Hence, notwithstanding the potentialities with which the above habits are fraught, they are probably not of great significance to other species on this area.

Seed and Fruit Feeders.—During most growing seasons plants of every description produce large quantities of fruits and seeds. These ripen in the fall and form a progressively diminishing food supply during the winter for certain ground-feeding birds and other animals. In the fall of 1935 on this 500 acres a collection of more than 90 species of such fruits and seeds was made. Only those were taken which appeared to be usable by winter birds as food or were listed by some author as such. Some fruits disappeared during the fall. Of those that were more persistent a record was kept of the length of time during the winter that they remained apparently available as a food supply for birds. Table 5 in the appendix gives the approximate abundance and duration of availability of 81 species. This represents the winter season of 1935-36 only and can not be taken as indicating the ordinary relative per-

FIG. 19. A 3-inch catalpa tree girdled by meadow mice. The upper limit of the bare area represents the snow level.

sistence of the various species. Some were buried under two feet of snow and others were almost entirely used up by the birds feeding upon them. In general, fleshy fruits disappeared early, leaving the dry fruits of grasses *(Poaceae),* buckwheats *(Polygonaceae),* and other common weeds found on cultivated ground as the most important winter foods of seed-eating birds and mammals. Cultivated grains were present in certain feeding stations and rye patches, but did not greatly interfere with the study of natural foods.

On the Kellogg Farm from point of size, the ringneck pheasant is the largest animal dependent upon grain and seeds in winter. That the species utilizes quantities of the common weed seeds as food has been shown by many investigators (Leffingwell, 1928; Forbush, 1929; Swenk, 1930; Beebe, 1931; Green and Beed, 1936; Dalke, 1937; Gigstead, 1937). A total of 70 fall and winter stomachs were obtained from hunters and by other means in this and near-by counties. A qualitative examination showed ragweed, green and yellow foxtail, several species of smartweed and bindweed, and other common weeds to be frequently taken. Corn and other cultivated grains were

present in quantities. The crop of a hen shot on February 3 contained rye, vetch, and dodder. Burdock, bittersweet, and grape were also often eaten in late winter.

The bobwhite quail utilizes similar foods in winter (Judd, 1905; Nice, 1910; Errington, 1930, 1931; Bird and Bird, 1931; Handley, 1931; Leopold, 1931). Eleven fall stomachs from this vicinity yielded quantities of ragweed, foxtail, panic grass, and buckwheat. Bobwhites are known to be particularly fond of legumes, and two of these stomachs contained the seeds of sweet clover (*Melilothus* sp.).

In the winter of 1935-36 a large portion of the natural food supply of the area was taken by flocks of songbirds. Tree sparrows and juncos were particularly abundant, and horned larks were common. The food habits of these birds have been studied by Judd (1898), McAtee (1905), Beal and McAtee (1912), and Gabrielson (1924). It has been fully demonstrated that common weed seeds form the bulk of their winter foods. A collection from this area of 124 stomachs (principally of juncos and tree sparrows) was made in December, January, and February. A qualitative analysis showed that 30 species of fruits and seeds had been taken as food. Following is a list of the 10 species most frequently taken and the number of stomachs in which traces or quantities of the food were found:

Ambrosia elatior (ragweed)	73
Chenopodium album (lamb's quarters)	54
Poa spp. (bluegrass)	27
Nepeta cataria (catnip)	23
Amaranthus retroflexus (redroot)	21
Monarda fistulosa (wild bergamot)	14
Rumex acetosella (sheep sorrel)	9
Amaranthus graecizans (tumbling pigweed)	8
Sporobolus spp. (dropseed grass)	8
Setaria lutescens (yellow foxtail)	7

Two other species of animals are of undoubted importance as feeders upon weed seeds. Although all mice appear to use this food to some extent, the white-footed mouse and prairie deer mouse are notable for the habit (Audubon and Bachman, 1849; Kennicott, 1856; Merriam, 1886; Seton, 1909; Cory, 1912; Nelson, 1918; Stoner, 1918; Bailey, 1926; Johnson, 1930; Gregory, 1936). As has been pointed out by Dice (1922) and Johnson (1926), a well-developed habitat selectivity is shown by these two species. The prairie deer mouse inhabits the open fields, and the white-footed mouse is a woodland form. On the Kellogg Farm one of the two is found everywhere except in very wet marsh. The prairie species is widely distributed in the open fields and grassland, while the woodland mouse inhabits all of the woods and brushland. The only habitat where both have been found is a grassy area sparsely planted to small conifers.

As a consequence of this habitat preference the food of *P. leucopus nove-*

boracensis contains a higher percentage of nuts and tree seeds than that of *P. maniculatus bairdii*. Osgood (1909) states that the former is very fond of basswood seeds, wild cherry pits, and acorns. Both species lay up winter stores, but both are also active foragers in all kinds of weather. From the standpoint of weed seeds all evidence points to the prairie deer mouse as the most important competitor of ground-feeding birds. A nest of this species that was excavated in January, 1937 contained approximately a pint of seeds of bush clover (*Lespedeza* sp.), ragweed, wheat, black bindweed (*Polygonum convolvulus*), yellow foxtail, campion (*Silene* sp.), and field sorrel. Tracks in the snow showed that this mouse regularly fed upon ragweed, tumbling pigweed, and lamb's quarters.

Two winters' observation on this area indicates that the intensity of competition for the above type of food depends principally upon the depth of winter snow. Deep snows quickly reduce the supply of available foods and concentrate the efforts of all species upon what remains. The nature of the growing season or other factors may determine the amounts of some foods that are produced. The drouth in 1936 evidently curtailed the crop of arrow-leaved tear-thumb and certain other species. However, the harvest from common weeds such as ragweed, lamb's quarters, amaranths, and others appears to be a very dependable quantity. These types made an excellent growth during the hottest part of the summer in 1936, when the ground was very dry and dusty four feet beneath the surface.

The very deep snow in the winter of 1935-36 rendered unavailable the low-growing foods such as field sorrel. Hence the dependence of nearly all seed-eating animals was upon ragweed, lamb's quarters, redroot (fig. 20), bergamot (fig. 21), and such other species as projected above the snow. Ragweed was the most abundant of these, and by the middle of February plants of this species had been almost completely stripped of their fruits. When such a condition was reached, the flocks of songbirds almost entirely left the area. Where before several hundred tree sparrows and juncos had not been unusual, hardly a bird was to be found. Errington (1930) refers to a season of deep snow when the ragweed supply was exhausted by the middle of January. In speaking of quail the same author (1931) calls attention to the "—terrific food competition furnished by small birds, ringnecked pheasants (in one area) and rodents—."

Considering the widespread and intensive activity of mice and songbirds, it appears that these animals took the greater part of the winter's supply of seeds. The fact that the mice stored food in quantities, and the ability of the songbirds to abandon the area if necessary leaves the pheasant and quail as the species most likely to suffer in case of food shortage. The shortage in February, 1936 did not last, as the deep snows melted late in that month. Pheasants found enough burdock, dodder, vetch, grape, bittersweet, and cultivated grains to satisfy their needs. Quail used such foods as sumac drupes

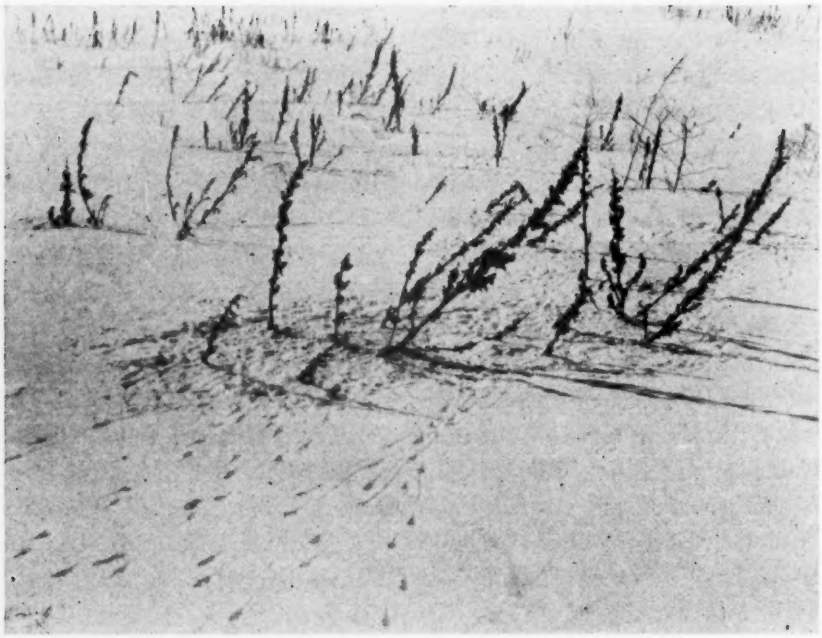

FIG. 20. Redroot upon which snow buntings fed above two feet of snow in February, 1936.

and ash samaras, or moved about until a feeding station, shocked corn (on near-by farms), or other supply was found. No starvation or decline in health was observed among the birds on the Kellogg Farm.

Evidently this is another relationship which, under some conditions, might seriously impinge upon two resident species, the pheasant and the quail. Under the conditions studied, however, the food shortage induced, in part, by mice and songbirds did not result in a loss of life among the game birds. In the following winter (1936-37) the supply of food available was much larger than in 1935-36, due to the small amount of snow on the ground. In that season very few songbirds were present; most of the pheasants and quail moved to adjoining sections of land; and the mice, evidently, were left in control of a food supply much in excess of their needs.

Mast Feeders.—One source of food on the area which should not be overlooked is the very large harvest of acorns which has been produced each fall. For three seasons this was one of the most abundant and important fall foods. White oaks produced little, red oaks slighly more, and black oaks very large quantities. In addition to being the most frequent species the black oak bears an acorn that is small enough to be readily swallowed by pheasants and ducks; whereas the other two species are rather large to be used until they are opened by squirrels, stepped upon, or otherwise broken up.

During October and November much of the mast harvest disappeared through the activities of fox squirrels, which stored away large numbers of acorns in individual holes in the ground. Mallard ducks took most of the

FIG. 21. Wild bergamot upon which tree sparrows fed in February, 1936.

supply near the water, and other birds such as blue jays and pheasants were active elsewhere. The chipmunk (Audubon and Bachman, 1849; Kennicott, 1856; Cory, 1912; Howell, 1929) and white-footed mouse also use quantities of this food. Korstian (1927) observed that from 90 to 100 percent of the total yearly supply of acorns is sometimes taken by animals. Squirrels and mice were found to be particularly important in this respect. There is no evidence from the present work that competition for the acorn harvest is ever acute, although by analogy a small crop and the exhaustion of the supply in the fall might mean privation to the fox squirrel in late winter.

Food Relations of Carnivores

The more that is learned of the food habits of animals the more omnivorous most species are found to be. Thus ground squirrels are known to feed extensively upon insects (Gillette, 1889; Orcutt and Aldrich, 1892; Bailey, 1893; McAtee, 1925), while such structurally authentic carnivores as the raccoon and skunk consume quantities of fruits, mast, and grain (Dearborn, 1932; Hamilton, 1936a). In the following discussion several species are

treated which, though primarily herbivorous, have certain significant carnivorous habits that make it logical to include them here.

Carrion Feeders.—As a food carrion appears to be most significant at the time of the melting of winter snows. Then all of the diseased and subnormal animals that succumbed to winter weather are revealed, and the increased activity of skunks and opossums certifies that the supply will not last long. Skunks in particular have been found to be lean and evidently hungry after more or less inactivity and are capable of eating large quantities of carrion. In one case a skunk carcass was found to have been almost entirely eaten (by skunks) in one night. Such remains are usually trimmed by mice, which also eventually destroy the bones that are left. It appears probable that in spring this is the principal source of animal food for such rodents as require it; and the calcium furnished by bones may well be important to pregnant females. In the winter of 1936-37 carrion was not covered by snow and was taken at any time animals were active; but in the winter of 1935-36 the sudden melting of deep snow in February rendered very noticeable the intensive use of this food by the species indicated. Crows feed upon carrion habitually and consume most of the carcasses of animals killed on the highways.

At the poultry plant of the Kellogg Farm several thousand chickens are reared on open range each year. At night after the chickens are housed female skunks and their young are often found in the poultry yard eating the chickens that have died of disease and other causes. It is not to be doubted that this supply of carrion is on this area an important source of food for young skunks. Twelve box traps were set in the chicken range on the night of July 17, 1936. In the morning nine skunks and a barn rat had been caught, and one of the other traps was sprung.

Predators of Small Mammals.—The small mammal key industry of the Kellogg Farm consists principally of six species: the thirteen-lined spermophile, meadow mouse, prairie deer mouse, white-footed mouse, short-tailed shrew, and prairie mole. In addition to these are the chipmunk, Cooper lemming-vole, pine mouse, jumping mouse, least shrew, and cinereous shrew; but the latter species are of such infrequent occurrence that they are probably of little ecological significance. The cottontail rabbit may be included in the small mammal key industry, but it appears more logical to discuss the species with animals of larger size.

The mammalian predators of this key industry on the farm studied are the skunk, weasel, house cat, opossum, and short-tailed shrew. The two first mentioned are doubtless of greatest importance. That the skunk is a pertinacious destroyer of mice, particularly Microtines, has been attested to by nearly all of the investigators who have touched upon the subject (Richardson, 1829; Kennicott, 1858; Merriam, 1886; Seton, 1909; Cory, 1912; Nelson, 1918; Stone and Cram, 1920; Cuyler, 1924; Dixon, 1925; Hatt, 1930; Johnson, 1930; Dearborn, 1932; Goodwin, 1935; Hamilton, 1935, 1936b). A

series of 99 skunk stomachs from fall, winter, and spring was collected during the present study.[17] Of these, 38 were empty or contained only trap debris. Of the remaining 61 stomachs, 12 contained the remains of mice, all of which were Microtus. These rodents formed 44.5 percent of the contents of the 12 stomachs and 8.7 percent of the contents of the total series of 61. One stomach was from December, 3 from January, 1 from February, 4 from March, and 3 from April. In a report on 62 skunk stomachs (three species) Lantz (1923) found that small mammals were most commonly taken from January to March. In an examination of 414 fecal samples from May to September Hamilton found 14.1 percent small mammals which were chiefly mice. In field work on this area it was very evident from fecal specimens and signs that feeding upon small mammals began as soon as skunks were active in spring, and continued into the summer. In August and September insects (grasshoppers and beetles chiefly) formed the bulk of material in droppings and later fruits became important. The significance of the above facts is manifest when it is considered that rodent populations are at a minimum in late winter and spring, and thus predation at this season is most effective in limiting the yearly increase.

Skunk diggings have been very common in tunnels of the prairie mole, and a skunk has been found in the daytime eating the remains of a mole (possibly carrion). It appears likely that on this area skunks are an effective check on mole numbers.

As mentioned previously, weasels are most effectively adapted to preying upon small fossorial animals. They are persistent enemies of such mammals as chipmunks, spermophiles, and all species of mice. The latter fact is supported by observations on this area as well as by a large mass of evidence accumulated by many investigators (Richardson, 1829; De Kay, 1842; Audubon and Bachman, 1849; Kennicott, 1857; Rhoads, 1903; Fisher, 1908; Wood, 1910; Cory, 1912; Dearborn, 1932; Hamilton, 1933, 1935; Goodwin, 1935; Errington, 1936). Of 15 weasel stomachs taken on and near this area 9 were empty. In all of the remaining 6 were found the remains of mammals. One contained flesh and fur of Sylvilagus, 2 of Microtus, and 3 of Peromyscus. All appearances indicate that the weasel may be the most effective check on the numbers of the spermophile on this area. These ground squirrels are abundant and strictly diurnal. In the daytime they remain close to the burrow and appear to be very alert and watchful. Thus it is doubtful whether a large number are taken by avian predators, although their habits protect them not at all from weasels (Bailey, 1926; Seton, 1929). Few mammals are known to eat the short-tailed shrew, though Nichols and Nichols (1935) write of shooting a weasel that was carrying one. There is probably no species of small mammal on this area that is not, at least occasionally, preyed upon by this carnivore.

[17] I am indebted to Dr. Clarence Cottam, In charge, and Mr. E. L. Nelson of Food Habits, Division of Wildlife Research, U. S. Bureau of Biological Survey, for arranging for the analysis of these stomachs in the laboratory at Washington.

In the winter of 1935-36 under deep snow small mammals appeared to be well protected from house cats. In the following winter, when very little snow was present, cat tracks were often found in Microtus colonies in the fields. During the latter season 18 cat stomachs were collected on this area, of which 3 were empty. In the 15 which contained food, Microtus remains (and one Synaptomys) occurred in 12 and formed 31.1 percent of the food. Evidently cats hunted such prey regularly during this winter season. These animals are known to kill many species of small mammals (Forbush, 1916; Van Hyning, 1931), although most authors point out that they take them much less often than birds (Bailey, 1923; Couch, 1928; Hatt, 1930). To date not enough food studies have been made on the cat to warrant conclusions as to the extent to which the animal feeds upon small mammals. However on this area appearances indicate that natural predators such as the skunk, weasel, and some birds are of much more importance in reducing their numbers.

The opossum is very omnivorous and eats many kinds of plant and animal food (Rhoads, 1903; Cory, 1912; Seton, 1929; Dearborn, 1932). Although they doubtless destroy some rodents, the extent to which opossums feed upon carrion renders evidence from stomach analysis very questionable. Of this species 30 stomachs were collected, during the study, principally in fall and winter. In this series 3 were empty and 7 contained remains of mice (Microtus). In the 27 stomachs that contained food these mice constituted 6.4 percent. One of the stomachs contained remains of a short-tailed shrew, though this may well be carrion, as these animals are often found dead (Emmons, 1840; Evermann and Clark, 1911). Evidently opossums prey upon mice to some extent, although, as few are present on this area, they probably are not a very important factor in reducing populations of these rodents.

There is considerable evidence that the short-tailed shrew is an enemy of mice (Merriam, 1886; Shull, 1907; Hahn, 1909; Nelson, 1918; Bailey, 1923; Anthony, 1928). Johnson (1930) states, "The short-tailed shrew, where it is abundant, is more important in the control of mice than all other natural enemies of mice combined." However in 244 stomachs examined by Hamilton (1930) only 4 contained mouse remains. In the present study shrews have often been taken in Microtus colonies during the winter and, from the amount of food required by this species, mice may well be a considerable item in the diet at times when insects are relatively unavailable.

The avian predators of small mammals are so well known that no lengthy treatment is needed here. The predaceous birds on the area that are important as enemies of the key industry are the marsh hawk, red-tailed hawk, screech owl, and great horned owl. From its abundance and persistent hunting the marsh hawk is doubtless of greatest importance. Red-tailed hawks have been few in number and not always present. The two owls probably take a large yearly toll. That small mammals form the bulk of the food of these birds

has been shown by the extensive work of Fisher (1893) and numerous contributions by other investigators (Bird, 1929; Cahn and Kemp, 1930; Errington, 1932, 1933; Pearson, 1933). Useful summaries of other work are given by Baldwin, Kendeigh, and Franks (1932), May (1935), and Bent (1937). During the fall migration season rough-legged hawks were frequently seen hunting on the Kellogg Farm and in 1934 one of these birds was seen by Mr. F. F. Tubbs to settle onto a pole trap with a mouse *(Microtus p. pennsylvanicus)* in its talons. In February, 1937 a Cooper hawk was observed tearing at a grass nest of the field mouse, and an investigation disclosed three young mice in the debris. On two occasions great blue herons have been seen at close range to catch meadow mice, and have often hunted in grassy meadows where these rodents were plentiful. The hunting technique was the same as that used on frogs and appeared to be effectual.[18] Fisher (1908) has observed a similar relationship between herons and rodents. Crows have also often been seen in and around meadow mouse colonies and have doubtless taken their share. The work of Barrows and Schwarz (1895) and Kalmbach (1918) has shown that small mammals form a considerable portion of the food of crows. That a part of such food is carrion is very probable. Evidence is good, however, that much of it is the result of direct predation. Judd (1902) also refers to the destruction of small mammals by crows.

The enemies of small mammals include practically every carnivorous species on the area. Couch (1928) has observed that, in general, predatory birds are more effective in destroying rodents than predatory mammals. There is, in the present study, no entirely reliable evidence upon which to base a conclusion; however from the numbers of skunks, weasels, and cats present, as compared with the numbers of marsh hawks, screech owls, and great horned owls, it appears that on the Kellogg Farm predatory mammals have been the most potent controlling force.

Predators of Larger Mammals.—The larger mammals of this area are here considered to be the cottontail, fox squirrel, weasel, skunk, opossum, and cat. Only one species of predator appears to kill all of these animals—the farm dog. Dogs have not been listed as a part of the fauna of the area as they are present only incidentally. On a few nights in winter dogs evidently hunted the area, and one rabbit is known to have been killed. Doubtless such hunting occurred at other seasons, but it was seldom observed. The dog has here been considered a part of the human factor, a standpoint that has not seemed justifiable in the case of the house cat, which is habitually feral.

As an animal community the Kellogg Farm is dominated by the great horned owl. Although I am not aware that this bird has been known to kill adult cats, it has been found to include in its diet all of the other species listed as larger mammals. Its food habits were studied by Fisher (1893), Bird (1929), Errington (1932), and English (1934b). On this area only two

[18] In both cases where herons were seen to catch a mouse the animal was taken to water and immersed before being swallowed.

pellets were found. One contained the neck vertebrae and feathers of a black duck (the kill was also found) and the other consisted of rabbit fur and bones. Two more pellets from a woods a few miles away contained rabbit remains. One rabbit kill was examined that can probably be ascribed to the horned owl. It appears, from the evidence at hand, that this owl may be one of the principal natural factors that reduce the winter population of the cottontail on this area. Various reports indicate that the great horned owl is one of the few species that prey upon the skunk (Audubon and Bachman, 1849; Wilkinson, 1913; Seton, 1929; Goodwin, 1935). On this area only one kill was found that might have been owl work, and evidence in the case was very unsatisfactory. In view of the continuous field work that was being done and the lack of any further indications, it appears that not many skunks were taken during this study.

The red-tailed hawk is the largest diurnal bird of prey found on the farm discussed and may be listed as an enemy of the rabbit, squirrel, and weasel (Fisher, 1893; Errington, 1932; Pearson, 1933; English, 1934a, 1934b). Other works are cited by May (1935) and Bent (1937). In this study on one occasion a red-tail flushed from the ground was seen to be carrying a fox squirrel in its talons. The marsh hawk is the most numerous hawk on the area in summer and probably accounts for many young rabbits and possibly some adults. It has also been demonstrated that the crow takes numerous young of this species (Barrows and Schwarz, 1895; Judd, 1902; Kalmbach, 1918). Several raided rabbit nests have been found in this work that pointed toward the crow as a possible predator.

Of the larger mammals the rabbit is most often preyed upon by other mammals. One of its principal enemies on the Kellogg Farm is the house cat. In the winter of 1935-36 two adult rabbits were killed, with very good evidence that the predators were cats. One rabbit was killed and partly eaten by a cat in a funnel trap set for pheasants. In the spring of 1936 one cat in Midland Park is known to have brought in two young rabbits. In his comprehensive work on the domestic cat Forbush (1916) states that they are very active in the pursuit of young and old rabbits and that they also kill squirrels. Seton (1909) and Linsdale (1928) cite other records of rabbits having been killed by cats. Being ground foragers, the skunk and opossum doubtless take numerous nests of young rabbits, although many of the remains found in stomachs may be classed as carrion. Skunk diggings have been found in close approximation to raided rabbit nests on this area, and Cory (1912) and Cuyler (1924) have included young rabbits in the list of the skunk's food. Kennicott (1858) and Brayton (1882) state that skunks capture adult rabbits by catching them in burrows. That the weasel also kills adult rabbits in holes is indicated by statements of Audubon and Bachman (1849) and Kennicott (1857). Fisher (1908), Seton (1929), and Stone and Cram (1920) also list the rabbit as weasel food. Hamilton (1935) found rabbit remains to con-

stitute 13.1 percent of the contents of a series of 360 fall and winter stomachs from New York State. Dearborn (1932) found that rabbits formed 14.29 percent of the mammalian food in 37 Michigan specimens. Flesh and fur of a rabbit were present in one of 15 weasel stomachs collected in this work and examined in the laboratory of the Biological Survey. That weasels can catch young rabbits in the open is shown by an observation of Leopold (1937). There is little evidence to indicate how great a factor the weasel has been in reducing rabbit numbers on the farm studied. It is evident that these carnivores took large numbers of mice, which were plentiful and easily captured. As a result I suspect that the number of adult rabbits killed is small, although young rabbits may well pay a heavier toll. In summary, it may be said that rabbits have formed a considerable part of the basic food supply of the larger carnivores found on this farm and as such, in common with the smaller rodents, were an important quantity in the food economy of the area.

Predators of Birds.—In the present work few data have been obtained on the summer predators of birds. At this season cats are numerous and probably kill birds regularly. The marsh hawk may also take a share in summer; and when the great horned owl is present, avian food is doubtless a part of its diet. Crows are known to kill young birds and are common on the Kellogg Farm at this season. The above are probably the most important summer predators of birds, although there is almost no actual evidence. As elsewhere pointed out, good observations in summer on some phases of field research are comparatively rare.

In winter the great horned owl and Cooper hawk were the only resident avian predators of birds. All evidence indicates that the screech owl was not important in this respect. In two pellets of the horned owl from a perch a few miles from the farm were the remains of a cock pheasant. Numerous feathers scattered about showed that the bird had been carried to a stub to be eaten. In three years at least three of these owls were taken on or near the farm under conditions indicating that they had been killing young or full-grown chickens. One is known to have killed a black duck. Bird remains were common in the food specimens analyzed by Fisher (1893), Errington (1933), and English (1934b). In spite of this evidence, the black duck above referred to is the only wild bird known to have been taken by a horned owl on the farm. Rabbits and other rodents have been more numerous than pheasants and quail, and appearances indicate that they have been the main sustenance of these owls.

The most important winter predator of birds on the Kellogg Farm during this investigation was the Cooper hawk. During the first winter of the work two adult pheasants (one in a funnel trap) were known to have been killed by these hawks (fig. 22). In the second winter and spring four known pheasant kills by Cooper hawks were recorded and one case was observed that was questionable. On several occasions old remains were found after carrion

FIG. 22. A hen pheasant killed by a Cooper hawk in lowland brush cover.

feeders had performed their offices and it was not possible to judge as to the original predator. In the six cases enumerated above hawks were actually flushed from the kill. In one case a bird returned at least six times to a dead pheasant. Kills of other species that were found where evidence indicated this hawk, were a meadowlark, a junco, and a cardinal. When it is considered that by no means all of the kills on such an area as this can be found immediately and some not at all, it is evident that the Cooper hawk has been a real limitation to pheasant numbers. During the second winter no quail were on the area much of the time and no predation at all was recorded for this species during the study. It has been shown that the Cooper hawk lives primarily upon birds as food and is particularly destructive to pheasants and quail (Fisher, 1893; Baldwin, Kendeigh, and Franks, 1932; Errington, 1933; English, 1934b). Since from one to five of these birds were present at all times throughout both winters, from this fact alone it would appear probable that considerable mortality occurred among the winter birds of the farm.

Among the mammalian predators of birds the cat was, from observations, the most efficient. It is very doubtful that weasels ordinarily take many birds,

and the skunk and opossum are little inclined to prey upon adults; so that at the Kellogg Farm in winter the domestic cat appeared to be practically the only important enemy on the ground. In the first winter of the work a cat entered a funnel trap and killed and partly devoured a cock pheasant. A hen in the same trap dashed herself to death in fright. In the following winter a cat killed two wing-clipped Mongolian pheasants at the sanctuary and carried them into the pines to be eaten. There are, from this work, no known cases of cats having killed birds in the wild, although several old remains were found to which no cause could be ascribed (and which may also have been due to Cooper hawks). I have no doubt, however, that cats have taken numerous birds and very probably pheasants on this area. The many records of cat predation cited by Forbush (1916) and others (Bailey, 1923; Hatt, 1930; Stoddard, 1931), as well as the consistent hunting by these animals in all kinds of weather, lend weight to this analogy.

Nest Predators.—The impacts of predators on bird populations through nest losses is one aspect of the predator-prey relations problem that can be studied, to some extent, quantitatively. The difficulty of evaluating an individual predatory species as a limiting variable to bird numbers makes it increasingly important that such a method be used on those parts of the problem that can be so treated.

In the spring and summer a fairly large number of mallard ducks nest around Wintergreen Lake and the swales on the sanctuary. In 1935 the history of 31 duck nests was followed and 11 of these were destroyed by predators. The losses could not be ascribed to individual species, as there were no reliable criteria by which to recognize the work of each. In the spring of 1936 a nest predation experiment was performed that was designed to indicate differences in the work of various predators. If the work of these animals could be recognized, the facts obtained could be applied to nests raided under natural conditions in the wild.

As population studies were in progress on the farm and it was not desirable to injure or kill any animals on the area, the study was made in the turkey marsh. Ten false nests of four or five hens' eggs each (incubator infertiles) were placed in a variety of cover situations. Around each nest were set four steel traps. The nest sets were run early every morning and were operated from March 19 to June 12—a total of 850 nest-nights. At first it was felt that, due to artificial conditions such as a scent trail to the nests and other factors which might affect predatory species differentially, the data gained could not be used quantitatively to indicate the relative amounts of nest destruction accomplished by each species. From the results, however, I believe that these factors were relatively unimportant. Stoddard (1931) came to the same conclusion with regard to predation on quail nests that were visited regularly in his studies. Nests that were checked frequently suffered no more from predators than those upon which few observations were made.

He states that in areas where human trails are frequent (as in the turkey marsh here referred to) ground predators probably do not habitually follow them.

In the trapping at nest sets the following animals were taken: 14 skunks, 9 crows, 8 fox squirrels, 5 opossums, 3 weasels, 3 blue jays, and 8 miscellaneous animals most of which were probably caught incidentally (a thrush, a turtle, etc.). Of these sets 29 were raided without the predator being identified, and 33 were disturbed with good evidence remaining as to the animal involved (fig. 28). Such evidence was hair in a trap, droppings, or very typical work on eggs. Of the cases which were identified on such a basis 9 were attributed to skunks, 15 to crows, 6 to squirrels, and 3 to opossums. For these four species of animals, then, the total cases of predation were: crow, 24; skunk, 23; squirrel, 14; and opossum, 8.

After comparing the shells of eggs eaten in certain proved instances of nest destruction, it was evident that in some cases the work of the four most important predatory species could be distinguished. Skunks commonly chewed a large hole in the shell, leaving the edge crushed and the membrane frayed. Well-defined tooth marks in eggs were relatively rare. Skunks usually scattered the egg shells from a nest out on one side for a distance of from 10 to 20 feet (fig. 24). Opossums have been found to munch up eggs, leaving the shells completely crushed. Opossum work could not, however, always be separated from skunk work. In the eight observed cases of opos-

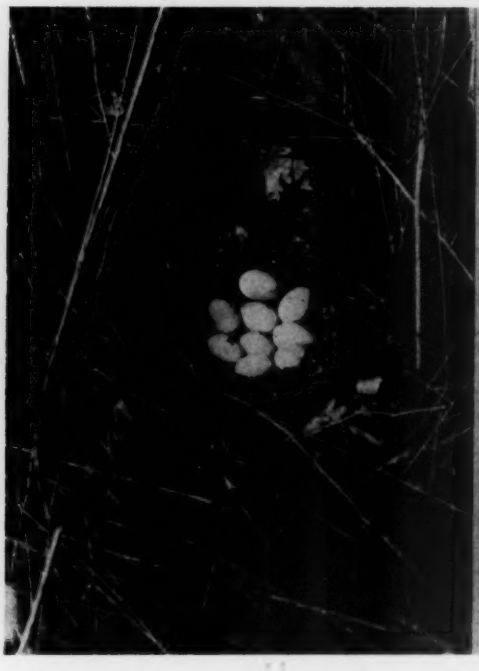

FIG. 23. Nest of mallard duck in lowland brush as it appeared on April 22, 1936.

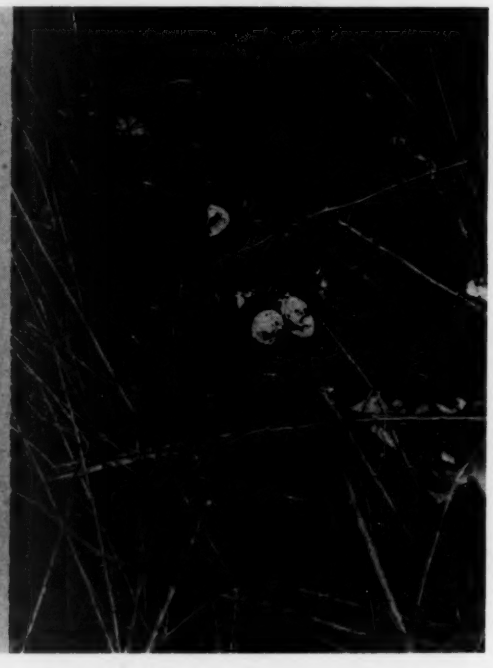

FIG. 24. The same nest as in fig. 23, on April 26, after being raided by a skunk.

sum predation the eggs were eaten in or within a few feet of the nest. Crows may split a cap neatly off one end of an egg (fig. 25), leaving no ragged edge or frayed membrane; or they may cut a groove or hole in one side. In the latter case the edges may be punched in, but are not crushed and ragged as in skunk work. Crows usually are unable to remove all the contents of an unincubated egg. They may also carry eggs away to be eaten elsewhere. Fox squirrel work was most typically represented by a neat cup left with the edges trimmed smooth and the contents licked out clean. The shells were usually left at the base of a tree (fig. 27) or on a stump. Shells left by squirrels and crows were sometimes similar.

It is to be emphasized that little can usually be inferred from a single egg. When an entire nest of eggs is eaten, however, their position noted, and the vicinity examined for other signs, a very good case may result.

In the application of this information to nests in the wild, 29 duck nests were studied in the spring of 1936. Of these, 10 were raided by predators. Three cases were identified as crow work, 2 as skunk, and 5 were unknown. Of seven pheasant nests checked, only one was raided—probably by an opossum, though possibly by a skunk. In the spring of 1937 records were obtained on 32 duck nests.[19] Of these, 17 were broken up by predators. Evidence was good that at least four were taken by crows and three by skunks. In most other cases evidence was poor. During this season, however, grackles were

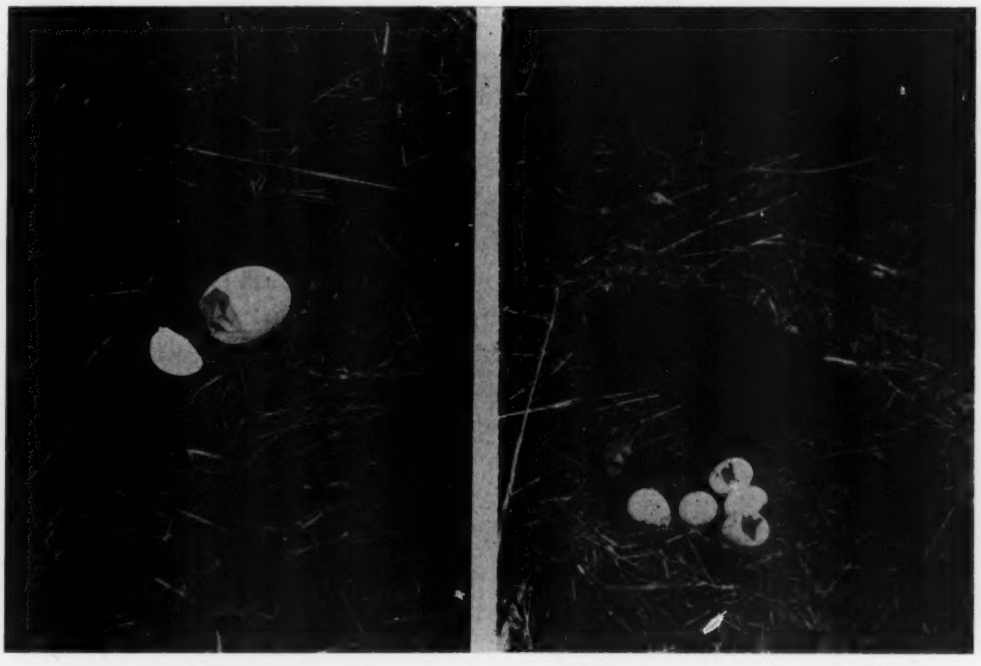

FIG. 25. A hen's egg after being eaten by a crow.

FIG. 26. A crow caught in steel traps at a false nest of hens' eggs.

[19] Most of the field work on this group of nests was done by Mr. Homer L. Bradley, who kept records and kindly called my attention to numerous cases of predation.

FIG. 27. Egg shells left at base of tree by a fox squirrel.

FIG. 28. A false nest raided by a skunk which escaped being caught but which left ample evidence of its identity. Arrow points to feces, which contained egg shells from a previous visit.

more numerous than usual, and several duck nests were found with some eggs that had small holes punched in them. It is very probable that these birds were responsible for a part of the losses, although there is little direct evidence. They were not known to have eaten eggs during the two years previous. Of a total of 99 nests (82 duck, 15 pheasant, 2 quail) observed in the wild during the three seasons 39 (38 duck, 1 pheasant) or 39.3 percent were broken up by predators. It is interesting to note that of 602 quail nests recorded by Stoddard (1931) 37 percent were destroyed by natural enemies. Hamerstrom (1936) found that 76.9 percent of 445 Iowa pheasant nests were unsuccessful, and that 19.3 percent of the losses could be attributed to predators. From the evidence available it appears that about one-third of the nests of ground-nesting birds were destroyed by egg-eating animals on the Kellogg Farm, and that such a rate of mortality may not be far from the usual loss suffered in such habitats. This can be more reliably judged when more data from other localities are available.

SUMMARY AND CONCLUSIONS

PURPOSE

The purpose of this study has been to demonstrate the approximate sizes and most vital interrelationships of the mammal and bird populations on 500 acres of farm land.

AREA

The area studied lies on an outwash plain in a recently glaciated region in southern Michigan. It includes Wintergreen Lake and five small kettle holes. The topography is somewhat irregular, varying between the 891- and 935-foot contours. About 277 acres have been cultivated.

In the order of their development in the hydrosere the plant habitats of this area may be listed as marsh, lowland brush, lowland woods, and upland woods. The stages of a secondary succession, starting with plowed ground, are also present here. The annual weed stage is found on cropland and, if undisturbed, will pass into the perennial weed and grassland stage. This, in time, becomes upland brush, which gives way to the upland oak woods.

This area resembles other surrounding farm land except for the ungrazed brush cover that has grown up in the lowlands and the coniferous plantings that have been made on the more hilly portions. An aggregate of about 20 acres of these plantings are present which vary in size from a few scattered trees to four acres of massed pines.

ANIMAL LIFE

The animal species of this area are discussed from the standpoints of abundance, habitat predilection, time of activity, and position in the food cycle. The summer and winter populations varied during the study to a marked degree owing to the fluctuation in numbers of resident animals and of migratory birds which were present during only a part of the year.

Population Studies

Censuses of mammals were taken principally by returns from trapping and marking. Winter burrow excavation was also used in the case of the skunk. Pheasants and quail were inventoried with bird dogs and by the interpretation of daily field work. Mice and shrews were taken in mouse traps baited with peanut butter. Quantitative studies have not been made on all species, and where figures are not available the comparative numbers present, as judged by indications, are given.

Rabbit.—Based upon the December kill and the number of individual rabbits trapped in January, February, and March the minimum population figure for December, 1935 was found to be 228. As judged by the number of individual rabbits taken in February and March the April population was about 25 pairs. In six weeks and five days, beginning on October 31, 1936, 102

rabbits were marked by trapping. On December 18, 19, and 20 a total of 126 rabbits were shot. Using the proportion of marked rabbits in the kill, the December population was calculated at 226 rabbits, or one animal per 2.1 acres.

Fox Squirrel.—In the fall and winter of 1935-36 sixty-one fox squirrels were marked by ear clipping. This constitutes an index population figure for about 30 acres of woodland (one squirrel per 0.49 acres). During the following summer the numbers of this species took a marked drop due, evidently to a mange-like disease that became epidemic. In the winter of 1936-37 only 39 individuals were taken.

Skunk.—During the first fall and winter 30 skunks were caught in the traps and marked. Of these, 20 were males. The sex ratio here is 0.5, and females are relatively inactive in winter. Hence if an equal number of females is presumed, the total number of skunks that are known to have used the area is about 40.

In the second fall and winter 29 male skunks and 15 females were taken in box traps. During the winter period of inactivity 19 burrows were excavated and two males and 16 females were handled that had not been taken in traps. Thus the total of skunks handled on this area was 62, or 31 males and 31 females. However, indications are that only 23 females occupied burrows on this area; and if there were an equal number of males, the total known resident winter population for the farm was 46 skunks, or one per 10.4 acres of land.

Ringneck Pheasant.—On a basis of bird dog censuses and daily field work the late fall population of 1935 was about 30 pheasants, or one bird per 16 acres.[20] In the following April the number was between 20 and 24. During the second winter many pheasants left the farm and gathered in a brushy area in the next section to the north. On January 22, 1937 only five pheasants were flushed in a census of the farm. Evidently numerous birds returned in the spring.

Bobwhite Quail.—Quail were censused in the same manner as pheasants. Populations were, however, even more variable due to movements. In December, 1935 the maximum number of bobwhite was observed when about 42 birls were on the area. Thus at this time the population density was about one quail per 11.4 acres. This species was much disturbed by the field work during the late winter period of deep snow. Evidently much shifting and splitting of coveys resulted from this factor. In the winter of 1936-37 a maximum of 10 quail were present and at times none at all was to be found.

Species of Lesser Abundance.—The winter weasel population, as judged by tracks, appeared to be about half a dozen individuals. On the same basis, from one to five cats were frequently on the area. The opossum population was small, evidently numbering three or four. In summer not more than two

[20] Population densities are calculated for 480 acres—Wintergreen Lake occupies 20 acres.

raccoons are known to have been present at one time, and there is only one fox record during this work. Woodchucks were uncommon on the farm, only three having been seen in three years. The winter Cooper hawk population evidently varied from one to five during two winters. The number of great horned owls was usually one and sometimes two.

Small Mammals.—Of the ground squirrels on the area the spermophile was abundant and the chipmunk comparatively uncommon. The most numerous small mammal was the prairie deer mouse, with the meadow mouse evidently second in numbers. The white-footed mouse, short-tailed shrew, and prairie mole were also common. Species of lesser importance were the star-nosed mole, masked shrew, least shrew, jumping mouse, Cooper lemming-vole, and pine mouse. The bulk of the small mammal key industry, then, was formed by the spermophile, prairie deer mouse, meadow mouse, white-footed mouse, short-tailed shrew, and prairie mole.

Animal Interrelations

Animal species interact chiefly by being associated in the same habitats and by being active at the same time. The most vital interrelationships arise through the necessity of every individual for food.

Habitat Relationships.—In summer herbaceous vegetation provides good cover everywhere and species like the cottontail, house cat, weasel, skunk, pheasant, and quail used nearly every part of the area. The fox squirrel and flying squirrel are restricted to woodland. The white-footed mouse was also found, but it includes brush areas and coniferous plantations in its habitat. In grassland the meadow mouse, spermophile, prairie mole, and prairie deer mouse were common, as were several species of sparrows and other birds. On cultivated ground the prairie deer mouse was the only permanent resident.

In winter the habitats of the squirrels, mice, and other species were the same as in summer except that meadow mice were often found in brush areas; and in the presence of snow, rabbits, pheasants, and quail were largely restricted to deciduous brush and conifers.

Activity Relationships.—The cottontail, fox squirrel, house cat, weasel, pheasant, and quail are designated predominants as they are active throughout the year. Among the smaller animals the prairie deer mouse, white-footed mouse, meadow mouse, and short-tailed shrew were the most common predominants. A large number of migratory birds were present only in summer and the raccoon was also found on the area studied only at this season. Resident animals that were active in summer but inactive during at least the coldest part of the winter are the skunk, opossum, woodchuck, spermophile, chipmunk, and jumping mouse. Common winter birds that were absent in summer are the Cooper hawk, junco, and tree sparrow. The great horned owl was regularly present in winter but appears to be only occasional in summer. The latter season is the time of greatest activity as all resident species are

active, as well as a large number of migrant birds. In winter the migrants are absent and several species of resident mammals are inactive.

Food Relationships.—Food relationships have been most easily studied in winter. It is at this season that supplies diminish and competition becomes most severe. Among herbivores field mice and rabbits were found to be the most typical feeders upon herbaceous plants; and when this food was covered with snow they subsisted upon bark. Potentially these two animals compete for this food supply and affect other species by reducing cover. On the Kellogg Farm, however, the amount of brush present was so large that neither of these relationships was vital in the winter of 1935-36. Another source of winter food for herbivores is the fruits and seeds of common weeds. Conditions of deep snow reduce the supply and bring about intensive competition between winter songbirds, pheasants and quail, and seed-eating mice such as the prairie deer mouse and white-footed mouse. A food shortage occurred in February, 1936. Through their habit of storing seeds mice probably did not suffer; the flocks of songbirds left the area; and pheasants and quail subsisted on other foods. The shortage was of brief duration, as snows melted in late February and exposed a new supply.

The carnivores on this area that feed on small mammals are the great horned owl, screech owl, marsh hawk, red-tailed hawk, crow, skunk, house cat, weasel, and opossum. The short-tailed shrew may be added as an enemy of mice.

The rabbit is the most important prey species among the larger mammals. It is taken by the horned owl, red-tailed and marsh hawks, crow, cat, skunk, weasel, and opossum. The fox squirrel is preyed upon by the red-tailed hawk, cat, and possibly the great horned owl and other species. The horned owl appears to dominate the community as it preys upon the skunk and thus utilizes larger food than any other predator on the area.

* * * * *

It is evident from this study that relatively dense populations of three species of large mammals have existed here together. The cottontail rabbit, the skunk, and the fox squirrel are abundant, and there is no apparent reason why they should not continue to thrive. Six species of small mammals are also particularly plentiful. The spermophile, prairie deer mouse, meadow mouse, white-footed mouse, short-tailed shrew, and prairie mole evidently find this farm a very favorable habitat.

Among birds the number of pheasants is low. The species has been conspicuously preyed upon by the Cooper hawk, but perhaps no more here than elsewhere. The drop in numbers from late fall to spring has been less than one-third, but the productivity of the breeding stock has been low. Evidently about one-third of the nests of pheasants are broken up by natural enemies. It is, however, not certain that the status of the bird can be attributed in any large measure to this factor, as such a proportion of nest losses may occur

even in favorable areas. The exact ways in which this environment is limited for pheasants have not been definitely established.

The large amount of cover makes this farm favorable to pheasants, rabbits, and other species in severe winter weather. The area also has been prolific of natural food supplies which supported large numbers of winter songbirds and other animals. The flora is very favorable to herbivorous species and hence the large, though probably not abnormal, numbers of small mammals found here are to be expected. It follows from this that the carnivorous species dependent upon the latter should also find the farm a favorable habitat. This is notably so in the case of the skunk; and the numbers of the weasel, cat, marsh hawk, redtail, horned owl, crow, and other carnivores are apparently about "normal" for these species.

On this area of farm land we have, in general, copious food supplies and abundant cover. The animal populations are characterized by large numbers of rabbits, squirrels, and skunks, but small numbers of pheasants. A knowledge of the consistency with which these relative numbers do or do not occur on other areas will throw further light upon the extent to which each of these species tends to determine the status of others.

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APPENDIX

CHECK-LIST OF VERTEBRATES

All of the species listed here have been recorded in Section 8, Ross Township, Kalamazoo County, Michigan, and nearly all were taken during the period from September, 1935 to June, 1937. For completeness the vertebrate fauna of Wintergreen Lake has been included, although the study has not dealt with "cold-blooded" forms. A total of 16 species of fishes, 12 amphibians, 12 reptiles, 162 birds, and 25 mammals have been recorded.

CLASS *PISCES*

Amia calva Linne	Bowfin
Erimyzon sucetta kennerlii (Lacepede)	Western lake chub-sucker
Notemigonus crysoleucas auratus (Rafinesque)	Western golden shiner
Notropis cornutus frontalis (Agassiz)	Northern common shiner
Notropis heterodon (Cope)	Black-chinned shiner
Notropis h. heterolepis Eigenmann and Eigenmann	Northern black-nosed shiner
Hyborhynchus notatus (Rafinesque)	Blunt-nosed minnow
Ameiurus n. nebulosus (Le Sueur)	Northern brown bullhead
Amieurus n. natalis (Le Sueur)	Northern yellow bullhead
Perca flavescens Mitchill	Yellow perch
Poecilichthys exilis Girard	Iowa darter
Huro salmoides (Lacepede)	Large-mouthed bass
Apomotis cyanellus (Rafinesque)	Green sunfish
Helioperca macrochira (Rafinesque)	Bluegill
Eupomotis gibbosus (Linne)	Pumpkinseed
Helioperca x *Eupomotis*	Bluegill x Sunfish hybrid

CLASS *AMPHIBIA*

Ambystoma maculatum (Shaw)	Spotted salamander
Bufo americanus Holbrook	American toad
Bufo fowleri Garman	Fowler toad
Acris gryllus (LeConte)	Cricket frog
Pseudacris triseriata (Wied)	Swamp tree-frog
Hyla crucifer (Wied)	Spring peeper
Hyla v. versicolor (Le Conte)	Common tree-frog
Rana cantabrigensis Baird	Wood frog

Rana catesbeiana Baird	Bullfrog
Rana clamitans Latreille	Green frog
Rana pipiens Schreber	Leopard frog
Rana palustris Le Conte	Pickerel frog

CLASS *REPTILIA*

Coluber constrictor flaviventris (Say)	Blue racer
Lampropeltis t. triangulum (Lacepede)	Milk snake
Natrix s. sipedon (Linne)	Water snake
Thamnophis sauritis (Linne)	Ribbon snake
Thamnophis s. sirtalis (Linne)	Common garter snake
Sternotherus odoratus (Latreille)	Musk turtle
Chelydra serpentina (Linne)	Snapping turtle
Emys blandingii (Holbrook)	Blanding turtle
Terrapene c. carolina (Linne)	Box turtle
Graptemys geographica (Le Sueur)	Map turtle
Chrysemys bellii marginata (Agassiz)	Western painted turtle
Amyda spinifera (Le Sueur)	Soft-shell turtle

CLASS *AVES*

Gavia i. immer (Brunnich)	Common loon
Podilymbus p. podiceps (Linne)	Pied-billed grebe
Phalacrocorax a. auritus (Lesson)	Double-crested cormorant
Ardea h. herodias Linne	Great blue heron
Casmerodias albus egretta (Gmelin)	American egret
Butorides v. virescens (Linne)	Eastern green heron
Nycticorax nycticorax hoactli (Gmelin)	Black-crowned night heron
Botaurus lentiginosus (Montagu)	American bittern
Ixobrychus e. exilis (Gmelin)	Eastern least bittern
Cygnus columbianus (Ord)	Whistling swan
Branta c. canadensis (Linne)	Canada goose
Branta bernicla hrota (Muller)	American brant
Chen h. hyperborea (Pallas)	Lesser snow goose
Chen caerulescens (Linne)	Blue goose
Anas p. platyrhynchos Linne	Common mallard
Anas rubripes tristis Brewster	Common black duck
Chaulelasmus streperus (Linne)	Gadwall
Mareca americana (Gmelin)	Baldpate
Dafila acuta tzitzihoa (Viellot)	American pintail
Nettion carolinense (Gmelin)	Green-winged teal
Querquedula discors (Linne)	Blue-winged teal
Spatula clypeata (Linne)	Shoveller
Aix sponsa (Linne)	Wood duck
Nyroca americana (Eyton)	Redhead
Nyroca collaris (Donovan)	Ring-necked duck
Nyroca valisneria (Wilson)	Canvasback
Nyroca marila (Linne)	Greater scaup duck
Nyroca affinis (Eyton)	Lesser scaup duck
Glaucionetta clangula americana (Bonaparte)	American goldeneye
Charitonetta albeola (Linne)	Bufflehead
Erismatura jamaicensis rubida (Wilson)	Ruddy duck
Lophodytes cucullatus (Linne)	Hooded merganser

Mergus merganser americanus Cassin	American merganser
Cathartes aura septentrionalis Wied	Turkey vulture
Accipiter v. velox (Wilson)	Sharp-shinned hawk
Accipiter cooperi (Bonaparte)	Cooper hawk
Buteo b. borealis (Gmelin)	Eastern red-tailed hawk
Buteo l. lineatus (Gmelin)	Northern red-shouldered hawk
Buteo p. platypterus (Vieillot)	Broad-winged hawk
Buteo lagopus s. johannis (Gmelin)	American rough-legged hawk
Aquila chrysaetos canadensis (Linne)	Golden eagle
Haliaeetus l. leucocephalus (Linne)	Southern bald eagle
Circus hudsonius (Linne)	Marsh hawk
Falco peregrinus anatum Bonaparte	Duck hawk
Falco s. sparverius Linne	Eastern sparrow hawk
Perdix p. perdix (Linne)	Hungarian partridge
Colinus v. virginianus (Linne)	Eastern bobwhite
Phasianus colchicus torquatus Gmelin	Ringneck pheasant
Rallus l. limicola Vieillot	Virginia rail
Porzana carolina (Linne)	Sora
Gallinula chloropus cachinnans Bangs	Florida gallinule
Fulica a. americana Gmelin	American coot
Oxyechus v. vociferus (Linne)	Killdeer
Philohela minor (Gmelin)	American woodcock
Capella delicata (Ord)	Wilson snipe
Actitis macularia (Linne)	Spotted sandpiper
Tringa s. solitaria Wilson	Eastern solitary sandpiper
Totanus melanoleucus (Gmelin)	Greater yellowlegs
Totanus flavipes (Gmelin)	Lesser yellowlegs
Pisobia melanotos (Vieillot)	Pectoral sandpiper
Pisobia minutilla (Vieillot)	Least sandpiper
Micropalama himantopus (Bonaparte)	Stilt sandpiper
Larus argentatus smithsonianus Coues	Herring gull
Larus philadelphia (Ord)	Bonaparte gull
Larus delawarensis Ord	Ring-billed gull
Hydroprogne caspia imperator (Coues)	Caspian tern
Chlidonias nigra surinamensis (Gmelin)	Black tern
Zenaidura macroura carolinensis (Linne)	Eastern mourning dove
Coccyzus a. americanus (Linne)	Yellow-billed cuckoo
Coccyzus erythropthalmus (Wilson)	Black-billed cuckoo
Tyto alba pratincola (Bonaparte)	Barn owl
Otus asio naevius (Gmelin)	Eastern screech owl
Bubo v. virginianus (Gmelin)	Great horned owl
Strix v. varia Barton	Northern barred owl
Chordeiles m. minor (Forster)	Eastern nighthawk
Chaetura pelagica (Linne)	Chimney swift
Archilochus colubris (Linne)	Ruby-throated hummingbird
Megaceryle a. alcyon (Linne)	Eastern belted kingfisher
Colaptes auratus luteus Bangs	Northern flicker
Centurus carolinus (Linne)	Red-bellied woodpecker
Melanerpes erythrocephalus (Linne)	Red-headed woodpecker
Sphyrapicus v. varius (Linne)	Yellow-bellied sapsucker
Dryobates v. villosus (Linne)	Eastern hairy woodpecker
Dryobates pubescens medianus (Swainson)	Northern downy woodpecker

Tyrannus tyrannus (Linne)	Eastern kingbird
Myiarchus crinitus borcus Bangs	Northern crested flycatcher
Sayornis phoebe (Latham)	Eastern phoebe
Empidonax t. trailli (Audubon)	Alder flycatcher
Empidonax minimus (Baird and Baird)	Least flycatcher
Myiochanes virens (Linne)	Eastern wood pewee
Otocoris a. alpestris (Linne)	Northern horned lark
Otocoris alpestris praticola Henshaw	Prairie horned lark
Iridoprocne bicolor (Vieillot)	Tree swallow
Riparia r. riparia (Linne)	Bank swallow
Stelgidopteryx ruficollis serripennis (Audubon)	Rough-winged swallow
Hirundo erythrogaster Boddaert	Barn swallow
Progne s. subis (Linne)	Purple martin
Cyanocitta c. cristata (Linne)	Northern blue jay
Corvus b. brachyrhynchos Brehm	Eastern crow
Penthestes a. atricapillus (Linne)	Black-capped chickadee
Baeolophus bicolor (Linne)	Tufted titmouse
Sitta c. carolinensis Latham	White-breasted nuthatch
Certhia familiaris americana Bonaparte	Brown creeper
Troglodytes a. aedon Vieillot	Eastern house wren
Telmatodytes p. palustris (Wilson)	Long-billed marsh wren
Cistothorus stellaris (Naumann)	Short-billed marsh wren
Dumetella carolinensis (Linne)	Catbird
Toxostoma rufum (Linne)	Brown thrasher
Turdus m. migratorius (Linne)	Eastern robin
Hylocichla mustelina (Gmelin)	Wood thrush
Hylocichla guttata faxoni (Bangs and Penard)	Eastern hermit thrush
Hylocichla ustulata swainsoni (Tschudi)	Olive-backed thrush
Hylocichla f. fuscesens (Stephens)	Veery
Sialia s. sialis (Linne)	Eastern bluebird
Regulus s. satrapa Lichtenstein	Eastern golden-crowned kinglet
Corthylio c. calendula (Linne)	Eastern ruby-crowned kinglet
Anthus spinoletta rubescens (Tunstall)	American pipit
Bombycilla cedrorum Vieillot	Cedar waxwing
Sturnus v. vulgaris (Linne)	Starling
Vireo flavifrons Vieillot	Yellow-throated vireo
Vireo olivaceus (Linne)	Red-eyed vireo
Vireo g. gilvus (Vieillot)	Eastern warbling vireo
Mniotilta varia (Linne)	Black-and-white warbler
Dendroica a. aestiva (Gmelin)	Eastern yellow warbler
Dendroica c. caerulescens (Gmelin)	Black-throated blue warbler
Dendroica coronata (Linne)	Myrtle warbler
Dendroica v. virens (Gmelin)	Black-throated green warbler
Dendroica fusca (Muller)	Blackburnian warbler
Geothlypis trichas brachidactyla (Wainson)	Northern yellowthroat
Setophaga ruticilla (Linne)	American redstart
Passer d. domesticus (Linne)	English sparrow
Dolichonyx oryzivorus (Linne)	Bobolink
Sturnella m. magna (Linne)	Eastern meadowlark
Agelaius p. phoeniceus (Linne)	Eastern redwing
Icterus galbula (Linne)	Baltimore oriole
Euphagus carolinus (Muller)	Rusty blackbird

Quiscalus quiscula aeneus Ridgway	Bronzed grackle
Molothrus a. ater (Boddaert)	Eastern cowbird
Richmondena c. cardinalis (Linne)	Eastern cardinal
Hedymeles ludovicianus (Linne)	Rose-breasted grosbeak
Passerina cyanea (Linne)	Indigo bunting
Spiza americana (Gmelin)	Dickcissel
Acanthis l. linaria (Linne)	Common redpoll
Spinus p. pinus (Wilson)	Northern pine siskin
Spinus t. tristis (Linne)	Eastern goldfinch
Pipilo e. erythrophthalmus (Linne)	Red-eyed towhee
Passerculus sandwichensis savanna (Wilson)	Eastern savannah sparrow
Ammodramus savannarum australis Maynard	Eastern grasshopper sparrow
Passerherbulus henslowi susurrans Brewster	Eastern Henslow sparrow
Pooecetes g. gramineus (Gmelin)	Eastern vesper sparrow
Junco h. hyemalis (Linne)	Slate-colored junco
Spizella a. arborea (Wilson)	Eastern tree sparrow
Spizella p. passerina (Bechstein)	Eastern chipping sparrow
Spizella p. pusilla (Wilson)	Eastern field sparrow
Zonotrichia l. leucophrys (Forster)	White-crowned sparrow
Zonotrichia albicollis (Gmelin)	White-throated sparrow
Passerella i. iliaca (Merrem)	Eastern fox sparrow
Melospiza l. lincolni (Audubon)	Lincoln sparrow
Melospiza georgiana (Latham)	Swamp sparrow
Melospiza m. melodia (Wilson)	Eastern song sparrow
Calcarius l. lapponicus (Linne)	Lapland longspur
Plectrophenax n. nivalis (Linne)	Eastern snow bunting

CLASS *MAMMALIA*

Didelphis v. virginiana Kerr	Virginia opossum
Scalopus aquaticus machrinus (Rafinesque)	Prairie mole
Condylura cristata (Linne)	Star-nosed mole
Sorex c. cinereus Kerr	Masked shrew
Cryptotis parva (Say)	Least shrew
Blarina b. brevicauda (Say)	Short-tailed shrew
Procyon l. lotor (Linne)	Raccoon
Mustela frenata noveboracensis (Emmons)	New York weasel
Mephitis nigra Peale and Beauvois	Eastern skunk
Vulpes fulva (Desmarest)	Red fox
Marmota monax rufescens Howell	Rufescent woodchuck
Citellus t. tridecemlineatus (Mitchill)	Thirteen-lined spermophile
Tamias striatus lysteri (Richardson)	Lyster chipmunk
Sciurus hudsonicus loquax Bangs	Southern red squirrel
Sciurus niger rufiventer (Goeffroy)	Fox squirrel
Glaucomys v. volans (Linne)	Eastern flying squirrel
Peromyscus maniculatus bairdii (Hoy and Kennicott)	Prairie deer mouse
Peromyscus leucopus noveboracensis (Fischer)	Northern white-footed mouse
Synaptomys c. cooperi Baird	Cooper lemming-vole
Microtus p. pennsylvanicus (Ord)	Eastern meadow mouse
Pitymys pinetorum scalopsoides (Audubon and Bachman)	Northern pine mouse
Ondatra z. zibethica (Linne)	Muskrat
Rattus norvegicus (Erxleben)	Norway rat
Zapus h. hudsonius (Zimmerman)	Meadow jumping mouse
Sylvilagus floridanus mearnsii (Allen)	Cottontail rabbit

TABLE 5. ABUNDANCE AND AVAILABILITY AS FOOD FOR BIRDS OF SOME FRUITS AND SEEDS IN THE WINTER, 1935-36

FLESHY FRUITS	APPROXIMATE DURATION OF AVAILABILITY				
	Nov.	Dec.	Jan	Feb.	Mar.
Aronia arbutifolia (Red chokeberry) (3)*	———	———			
Aronia melanocarpa (Black chokeberry) (3)	———	———			
Celastrus scandens (Bittersweet) (2)	———	———	———	———	———
Cornus amomum (Silky dogwood) (1)	———	———			
Cornus candidissima (Gray dogwood) (1)	———	———			
Cornus florida (Flowering dogwood) (3)	———	———			
Cornus stolonifera (Red-osier dogwood) (1)	———	———			
Crataegus (Hawthorn) (2)	———	———	———		
Evonymus atropurpureus (Wahoo) (3)	———	———			
Ilex verticillata (Michigan holly) (3)	———	———	———		
Juniperus communis depressa (Ground juniper) (3)	———	———	———		
Lonicera caerulea (Mountain fly honeysuckle) (3)	———	———	———	———	
Lonicera japonica (Japanese honeysuckle) (3)	———	———	———	———	———
Malus coronaria (Wild crab) (3)	———	———	———	———	———
Parthenocissus quinquefolia (Virginia creeper) (2)	———	———	———		
Phytolacca americana (Pokeberry) (2)	———	———	———	———	
Polygonatum pubescens (Solomon's seal) (3)	———	———	———	———	
Prunus serotina (Wild black cherry) (2)	———				
Rosa sp. (Rose) (1)	———	———	———	———	———
Rhus copallina (Shining sumac) (1)	———	———	———	———	———
Rhus glabra (Smooth sumac) (1)	———	———	———	———	———
Rhus typhina (Staghorn sumac) (1)	———	———	———	———	———
Sambucus canadensis (Elderberry) (1)	———	———			
Smilacina racemosa (False Solomon's seal) (3)	———	———			
Smilax herbacea (Herbaceous smilax) (3)	———	———	———	———	
Smilax hispida (Hispid smilax) (3)	———	———	———	———	
Solanum carolinense (Horse nettle) (3)	———	———	———	———	
Solanum dulcamara (Bittersweet nightshade) (1)	———	———	———	———	
Solanum nigrum (Black-berried nightshade) (3)	———				
Sorbus americana (Mountain ash) (3)	———	———	———		
Symphoricarpos racemosus (Coralberry) (3)	———	———	———		
Viburnum acerifolium (Maple-leaf viburnum) (3)	———				
Viburnum lentago (Nannyberry) (3)	———	———			
Viburnum opulus americanum (High-bush cranberry) (3)	———	———	———	———	———
Vitis vulpina (Wild grape) (1)	———	———	———	———	———
DRY FRUITS AND SEEDS					
Amaranthus graecizans (Tumbling pigweed) (2)	———	———	———	———	
Amaranthus retroflexus (Redroot) (1)	———	———	———	———	
Ambrosia elatior (Ragweed) (1)	———	———	———	———	
Arctium minus (Burdock) (1)	———	———	———	———	———
Bromus tectorum (Brome grass) (2)	———	———			
Carex sp. (Sedge) (2)	———	———	———		
Cephalanthus occidentalis (Buttonbush) (1)	———	———	———	———	———
Chenopodium album (Lamb's quarters) (1)	———	———	———	———	
Cuscuta pentagona (Dodder) (2)	———	———	———	———	———
Echinochloa crusgalli (Barnyard grass) (3)	———	———	———		
Echinocystis lobata (Wild cucumber) (3)	———	———	———		
Fraxinus americana (White ash) (2)	———	———	———	———	———
Lespedeza hirta (Bush clover) (3)	———	———	———		
Lychnis alba (White cockle) (3)	———	———	———		
Melilotus alba (White sweet clover) (1)	———	———	———	———	
Monarda fistulosa (Wild bergamot) (1)	———	———	———	———	
Monarda punctata (Horse mint) (3)	———	———	———		
Nepeta cataria (Catnip) (2)	———	———	———	———	
Oenothera biennis (Evening primrose) (2)	———	———	———		
Panicum capillare (Old witch grass) (2)	———	———			
Plantago aristata (Bracted plantain) (3)	———	———	———		
Plantago major (Common plantain) (1)	———	———	———		

*Relative frequency as judged by field observations: (1)-abundant; (2)-common; (3)-less common.

TABLE 5. *(Continued)*

FLESHY FRUITS	APPROXIMATE DURATION OF AVAILABILITY				
	Nov.	Dec.	Jan	Feb.	Mar.
Poa pratensis (Kentucky bluegrass) (1)	———	———	———		
Polygonum acre (Smartweed) (3)	———	———	———		
Polygonum coccineum (Water smartweed) (2)	———	———	———		
Polygonum convolvulus (Black bindweed) (2)	———	———	———	———	———
Polygonum hydropiper (Water pepper) (2)	———	———	———		
Polygonum orientale (Prince's feather) (3)	———	———	———		
Polygonum persicaria (Lady's thumb) (1)	———	———	———		
Polygonum sagittatum (Arrow-leaved tearthumb) (1)	———	———	———		
Polygonum scandens (Climbing false buckwheat) (2)	———	———	———	———	———
Prunella vulgaris (Self heal) (2)	———	———	———	———	———
Quercus alba (White oak) (2)	———	———	———		
Quercus borealis maxima (Red oak) (1)	———	———	———		
Quercus velutina (Black oak) (1)	———	———	———		
Robinia pseudo-acacia (Black locust) (3)	———	———	———	———	———
Rumex acetosella (Sheep sorrel) (1)	———	———	———		
Rumex altissimus (Tall dock) (3)	———	———	———	———	———
Rumex crispus (Curled dock) (2)	———	———	———	———	———
Rumex obtusifolius (Broad-leaved dock) (2)	———	———	———	———	———
Rumex verticillatus (Swamp dock) (3)	———	———	———	———	———
Setaria lutescens (Yellow foxtail) (1)	———				
Setaria viridis (Green foxtail) (3)	———	———	———		
Steironema ciliatum (Fringed loosestrife) (3)	———	———	———	———	
Verbena hastata (Blue vervain) (2)	———	———	———	———	
Verbena urticaefolia (White vervain) (2)	———	———	———	———	

THE STRUCTURE AND DEVELOPMENT OF OLD FIELD SHORTLEAF PINE STANDS AND CERTAIN ASSOCIATED PHYSICAL PROPERTIES OF THE SOIL[1]

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THE STRUCTURE AND DEVELOPMENT OF OLD FIELD SHORTLEAF PINE STANDS AND CERTAIN ASSOCIATED PHYSICAL PROPERTIES OF THE SOIL

INTRODUCTION

Since the publication of Cowles' (1899) epochal work on the developmental nature of the plant communities of the Lake Michigan sand dunes, there have been countless studies of plant succession. Although successional studies have been carried on in almost all countries, this phase of ecology has been the particular province of the American workers led by such exponents of the dynamic theory of change as Clements, Cooper, Nichols, and others. Of necessity, many of the conclusions have been based on purely observational rather than quantitative data and have largely concerned only the changes in the vegetation itself. A few investigations have been made on the successional relations of such habitat factors as hydrogen-ion concentration, evaporation, and soil moisture.

European investigations have long been directed toward exact quantitative information concerning the vegetation of existing plant communities. In an attempt to explain the "raison d'être" of such communities, an intensive study of the environment, the edaphic phase in particular, has developed in conjunction with these quantitative vegetational analyses. It is only within the last few years that such studies have become prominent in American literature.

In the Piedmont region of North Carolina, much abandoned agricultural land is reverting to forest. In the early stages of this succession, pine is an almost universal dominant. This old field pine is very important economically and a quantitative knowledge of the mutual effects of pine vegetation and soil, during succession, would be of importance not only from a purely ecological standpoint but might also have many applications in the field of silviculture. With this in mind, detailed investigations of the vegetation and the soil were made on an old field successional series of shortleaf pine (*Pinus echinata* Mill.) stands in the Duke Forest in Durham County, North Carolina. The present study, then, is an attempt to apply quantitative phytosociological methods of vegetational analysis to the communities in a successional series and to correlate statistically these results with exact measurements of habitat factors, namely, certain physical properties of the soil.

HISTORICAL REVIEW

As has been previously pointed out, relatively little work has been done on the interrelationships between the physical properties of soil and the

change in vegetation during succession. For the most part, the investigations have been confined to the changes in the chemical make-up of soil as influenced by plant cover and the resultant effect on type of flora. The greater part of the work in this latter category has been confined to the change in the hydrogen-ion concentration of soil and its effect on the species present and on profile characteristics.

Schneider (1927), Griffith, et al. (1930), and others have shown that there is an increase in the acidity of the soil under pure pine stands with increasing age of the stand. This would undoubtedly be true also for the shortleaf pine stands in the Duke Forest, since Coile (1933) has found that the highly acid litter under shortleaf stands in the Forest increases the active acidity in the underlying mineral soil. It would seem reasonable then that the active acidity in the mineral soil would increase with age of stand due to the addition of the products of pine litter to the soil.

It has been demonstrated that this highly acid condition of litter causes a podsolized soil to develop under pine stands in climatic mull regions due to excessive leaching of iron and aluminum sesquioxides (Fisher, 1928; Stickel, 1928; Griffith, et al., 1930). Aaltonen (1928) has shown that this greater amount of leaching under forest stands, as compared to open fields, also tends to wash the available calcium and phosphoric acid deeper into the soil. He also found that, as a result of leaching, there was a slightly lower percentage of the smaller soil fractions in forest soils than in those of open fields.

In 1849, Jules Thurmann suggested that the physical factors of soils are far more important in relation to plant growth than are chemical properties. He believed that it is the physical structure of soil that regulates the distribution of species because of the interrelationships of structure and moisture conditions of soil. His theory has been subject to much discussion and, while it has its fallacies, it still holds true from the standpoint of forest soils. This greater importance of physical factors of forest soils over chemical constitution in regard to site quality has been stressed by Henry (1908), Kraus (1911), Toumey and Korstian (1937), and others.

While little has been published concerning the effect of vegetation on physical properties of soil during actual forest succession, there have been many investigations, mainly European, on physical differences between forested and cleared land. Outstanding contributions are those of Ramann (1897), Hoppe (1898), Albert (1912a, 1912b, and 1913), Engler (1919), Tschermak (1920), Burger (1922, 1929), Stewart (1932), and Auten (1933). Their results show that forest soils are much lighter and more porous than are those of cleared land. In a forest soil, the air capacity, water-holding capacity, and percolation rate tend to be higher, while volume-weight tends to be lower than in soil of any type of cleared land. These differences are mainly attributable to the greater number of root channels, more abundant soil fauna, and the large amount of accumulated organic matter under forest vegetation.

The recovery of these properties through revegetation has been relatively little investigated. Berkmann (1913) appears to have been the first to point out that soil structure was appreciably changed by the roots of plants growing in it. He found that this effect was greater in a clay soil than in a sandy type. In further studies he showed that meadow soils had a higher percolation rate than crop or barren soils because of the greater number of root systems. This effect of plant associations and their roots on soil, with special regard to plant succession, has been stressed by Meyer (1922). He emphasized the importance of the earlier stages in succession in the preparation of soil for plants which invade later and those which eventually make up the climax community. The pioneer plants tend not only to add humus to soil but their root channels give the soil better aeration. Auten (1933) says that a large degree of soil porosity was found to be regained 20 to 25 years after plantations of forest trees had been established on cultivated lands.

In central Europe, Aichinger and Siegrist (1930), studying air capacity of soil in relation to succession, pointed out that the appearance of the assembly of plants such as Convallaria, Maianthemum, Paris, and Oxalis on the floor of mixed forest was accompanied by an increase in air capacity of soil from 8 to 23 percent. The use of such herbaceous plants to indicate the physical nature of the forest soil is the basis of the Finnish forest type classification (Cajander, 1926). More recent work on the indicator value of certain plants in expressing the development of physical properties of forest soil has been produced by Berger (1934) and Gassert (1936).

While the quadrat method has been used many times in quantitative studies of vegetation during succession, such data have been subjected only rarely to a statistical phytosociological analysis. Dziubaltowski's (1918) investigation of the succession following the cutting of the Quercus-Carpinus forest in southern Poland is one of the few examples of this type of work. Dziubaltowski used the floristic-statistical methods of Jaccard (1902) and came to the conclusion that Jaccard's frequency curves best expressed the trend of succession. Braun-Blanquet and Jenny (1926) used the statistical phytosociological methods of Braun-Blanquet and Pavillard (1925) in working out the development of vegetation and soils in the central Alps. Among American workers who have applied phytosociological methods to the analysis of succession are Cooper (1922) in New England and Cox (1933) on alpine succession in Colorado.

PLAN OF STUDY

In any study of succession involving long periods of time, a great many of the conclusions must be reached by inference, that is, comparing areas of similar topography, climate, and soils in different stages of vegetative development. This method necessitates the choosing of comparable locations for investigation; stations which would be practically identical as regards the strictly physical factors of environment if there were no plant coverings.

It was planned to study the interrelationships of vegetation and physical factors of soil throughout the pine stage of old field forest succession and, for the reasons stated above, on areas as identical in physical environment as it is possible to find in nature. Climate (macroclimate) was first eliminated as a variable by limiting the stands to a very small part of Durham County, North Carolina. Specifically, the stands were located in the eastern portion of the Durham Division of the Duke Forest within an area of approximately 1.3 square miles. It is included within a rectangle of which the boundaries are State Highway 751 on the north, Sand Creek on the east, Cornwallis Road on the south, and Rigsbee and Erwin Roads on the west. Korstian and Maughan (1935) have described the climate of the Duke Forest, including the area under investigation.

The area lies wholly in the Durham Triassic Basin, the soils of which are quite varied. The majority are derived from sedimentary Triassic sandstones, mudstones, and shales, while a few are developed from igneous dikes and sills. In order to eliminate the variability of soils as a factor, it was decided to confine the problem to a single soil type if possible. Being least frequently eroded, the Granville sandy loam was selected from available types as being the most desirable for this study. According to Perkins, et al. (1924), Granville sandy loam has a grayish or yellowish surface soil and a subsoil of yellow or reddish sandy clay to clay. It is derived from the sandstones, mudstones, and shales of Triassic age and is often found surrounding igneous dikes and sills.

The topographical factor was minimized by selecting only those stands which were on level or nearly level areas. In several of the stands there was a slight slope, in all cases toward the south.

With the strictly physical factors of habitat being thus delimited to practically level areas of Granville sandy loam within a region of approximately one square mile, the next problem was to find a series of pine stands on these areas, ranging from recently abandoned cultivated lands with a few scattered seedlings to mature pine with a good undergrowth of hardwoods. To eliminate the effects of uneven stocking or partial cutting on physical properties of soil (Burger, 1927), only fully stocked stands which had been almost entirely free from cutting were considered. Since Lönnroth (1925), Von Pöntynen (1929), and Aaltonen (1934) have all pointed out that in pure coniferous stands there is a higher stem count of dominants on the better sites and a correspondingly low count of undergrowth, the present work was confined to the stands of better site quality in order to eliminate any error in density of vegetation due to inequalities in site. The site indices for shortleaf pine in the stands finally selected ranged from 66 to 80. These are stated as the amount of height growth for the species in 50 years. They were determined by height measurements of the dominant trees by members of the Duke Forest staff. There are no available recorded indices for the younger

stands because such indices calculated from height of trees are not reliable for stands of the younger age classes. However, these stands are on essentially similar sites as is shown by the fact that the ratio between the amount of colloids in the B_1 horizon and the depth of surface soil is practically the same for these stands as it is for the older stands. This is based on the work of Haig (1929) and Coile (1935) who have shown that there is a definite correlation between these soil factors and site index.

After examining all the stands in the area, a series of eight locations, all meeting the above requirements, were selected. These ranged from a field, abandoned about 5 years, to a mature pine stand in which the dominants averaged 110 years of age. All of these stands were even-aged and had seeded in naturally on abandoned fields. The abandoned field used in the study was in the Andropogon stage of development (Oosting, 1933 and Crafton and Wells, 1934) and there were a few scattered shortleaf pine seedlings. The appearance of this field at the time of investigation is illustrated in Fig. 1. The seven pine stands were of the following ages: 9 years, 13 years, 21 years, 31 years, 56 years, 83 years, and 110 years. Interior views of the 13 year, 31 year, and 110 year examples are presented in Figs. 2, 3, and 4, respectively. Extensive search revealed that these stations are practically the only shortleaf pine stands on Granville soil in the western part of Durham County which are as yet little changed from the natural condition. The age of the stand is the average obtained from increment borings of ten dominant pines in each stand.

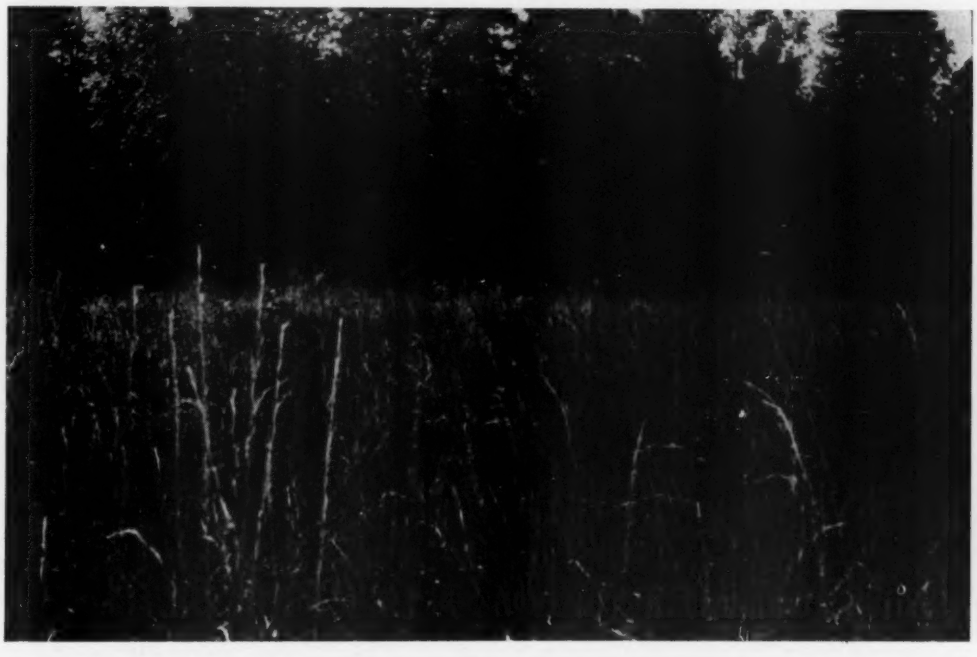

FIG. 1. The old field as it appeared at the time the study was made. *Andropogon virginicus* is the dominant.

Extensive search was made throughout Durham County for a young oak stand which had originated on Granville soil following shortleaf pine. It was thought that vegetational studies on the successor to the pine community

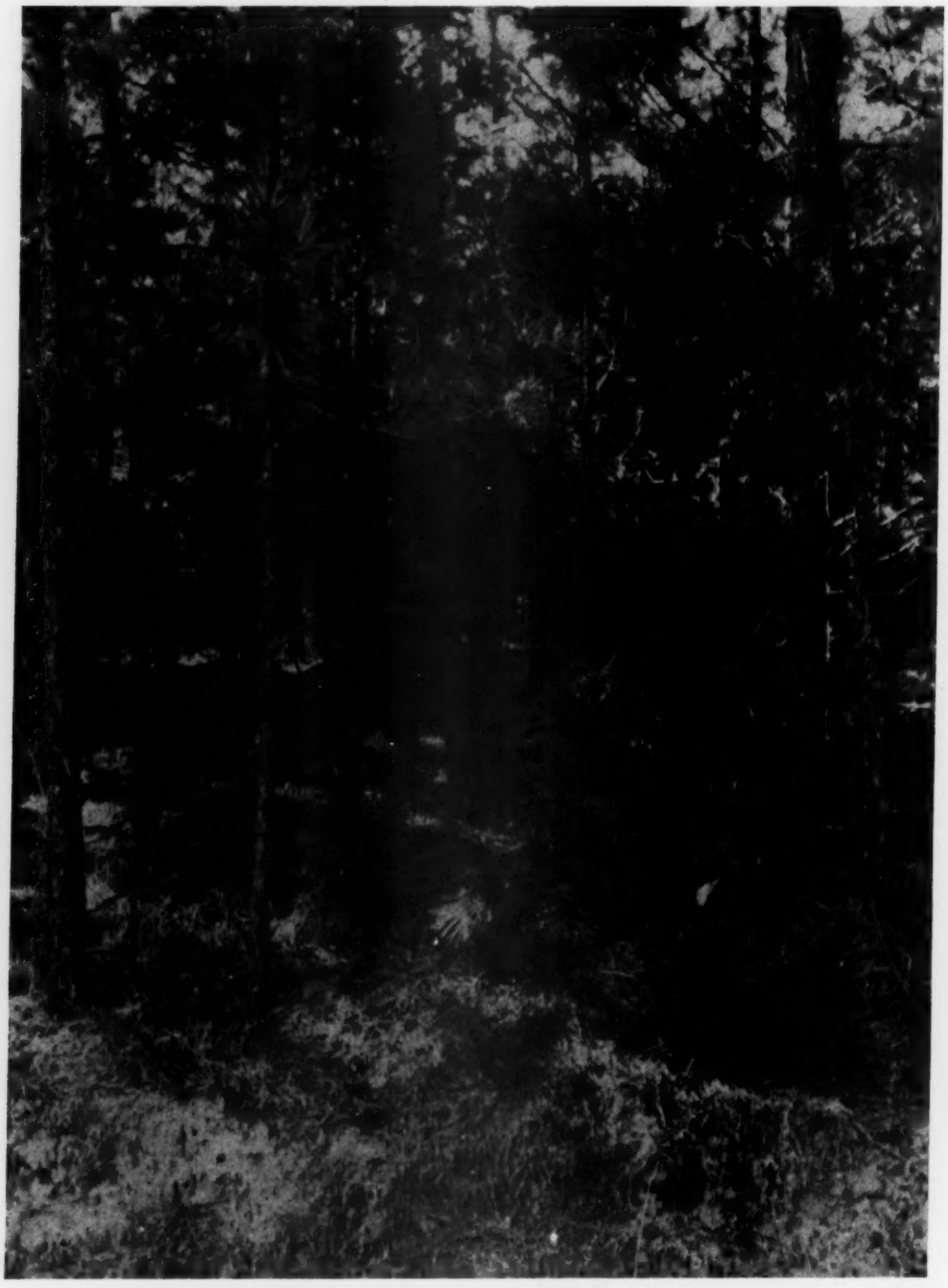

FIG. 2. An interior view of the 13-year old stand. Note the crowded condition of this stand and the already thick accumulation of needles on the ground.

might yield interesting results comparable to those found in New England by Fisher (1928) and Griffith, et al. (1930). Such a study might also throw some light on the question of climax communities of the Piedmont plateau.

FIG. 3. An interior view of the 31-year old stand. Note that although the dominant pines are fewer than in the younger stands, the forest floor is quite barren of vegetation. Notice also the still-visible furrows as brought out by the undulating tree shadows.

The attempt was without success, however, as it seems that the Granville soils are much too important agriculturally to be given over to the growing of timber, especially the slowly growing varieties.

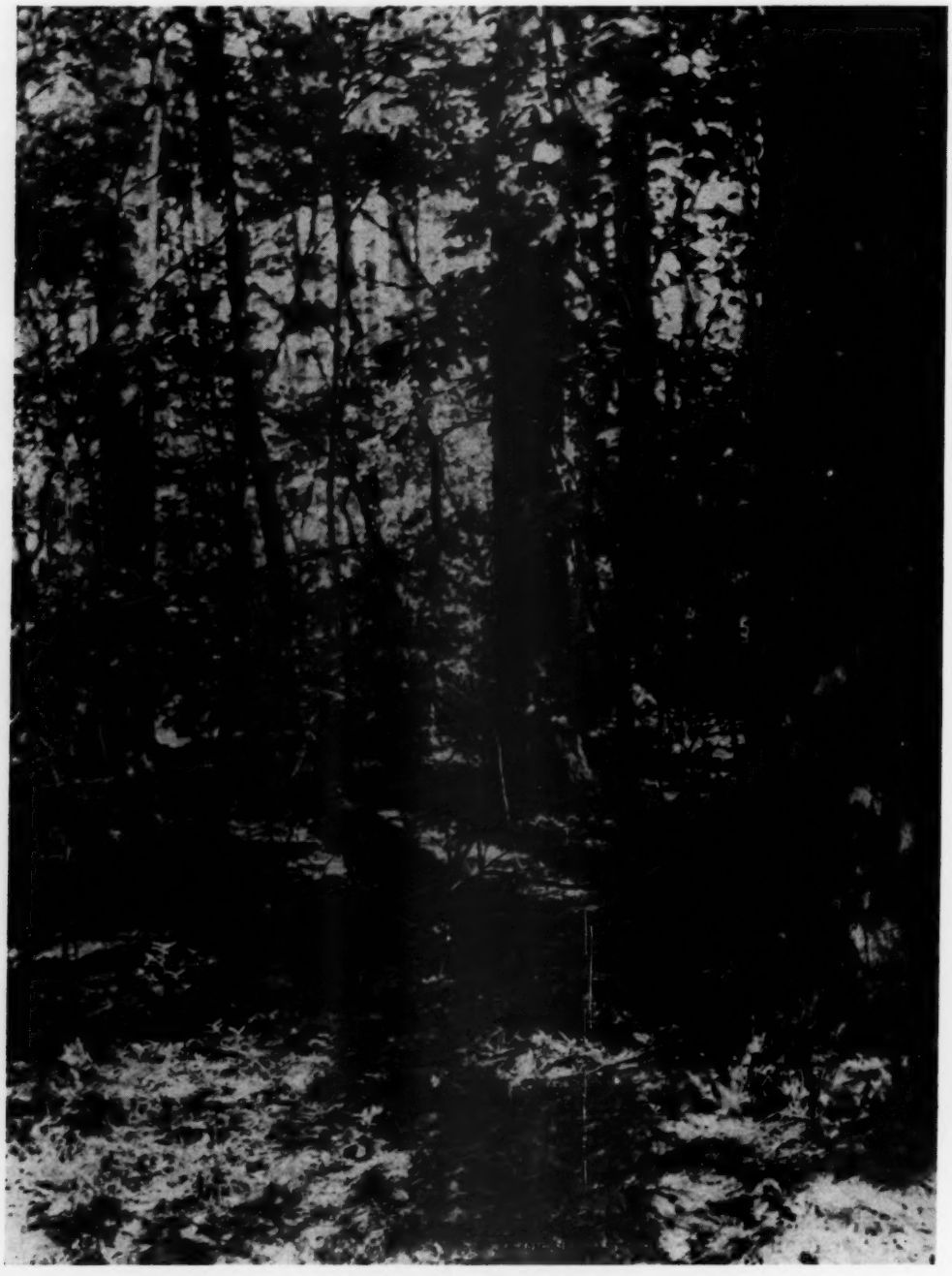

FIG. 4. An interior view of the 110-year old stand. The mature pines here are relatively far apart as compared to the younger stands and the forest floor is covered with a luxuriant undergrowth of young oaks and other hardwoods.

METHODS OF INVESTIGATION

VEGETATION

The vegetation of the various stands was studied quantitatively by the quadrat method. Count-lists were made for each vegetational stratum: the first being made up of the dominant, subdominant, and secondary trees; the second of the shrubs and woody reproduction; and the third of the herbaceous flora. As Cain (1934) has pointed out, size of quadrat is extremely important in such an investigation and the minimum area sampled in a community or in each stratum is dependent on the nature of that community or stratum. Among the methods for determining minimum quadrat size which Cain puts forth is the use of "percentage of total flora-to-area sampled" curves. In this procedure, the percentage encountered of the total species of the stand is plotted against the quadrat size or area sampled. The point at which the curve flattens most strongly is taken to be the minimum quadrat area. Cain worked only on the vegetation as a whole but he emphasized the fact that a separate investigation should be carried out for each vegetational stratum to determine the best quadrat size for that stratum.

With this in mind, a preliminary survey was made of the 110-year old stand to determine the size of quadrat which was most suitable for each layer. An intensive survey was first made of the whole area, which consisted of 4.62 acres, to compile a complete floristic list of the dominants, secondary trees, shrubs and "transgressives" (woody reproduction under 7 feet in height, Cain, 1934), and herbs. The first two strata were considered together because of the fact that practically the only dominant was pine and it was thought best to study pine and the secondary understory on the same quadrats for purposes of comparison. Ten sets of five quadrats each were distributed, widely and evenly, through this stand. In the same set, each quadrat included all the quadrats smaller than itself. The quadrats were of the following sizes: ¼ milacre, ½ milacre, 1 milacre, 4 milacres, and 25 milacres, with the smaller sizes being nested in one corner of the largest plot. A milacre is an area 6.6 feet on a side (0.001 acre) and was employed because of its extensive use by foresters.

Count-lists of dominant and secondary trees were made on all quadrats; of shrubs and transgressives on the four smaller sizes; and of herbs on the three smaller sizes. The results of this survey are shown in Tables 1, 2, and 3. Using the data included in these tables, species-area curves were plotted for each stratum. Hanson and Love (1930) and Cain (1934) suggest using the quadrat size at which a species-area curve breaks most strongly. Such a curve for the herbaceous flora breaks most strongly at the ¼-milacre size (approximately 1 square meter). This size was therefore adopted as being suitable for the herbaceous layer both from the standpoint of sampling and the amount of labor involved. Curves for the arborescent flora and for the

shrub and reproduction layer show breaks at the 4-milacre and ½-milacre sizes, respectively. However, in determining the frequency indices (Raunkiaer, 1918) on the various sized plots, it was found that on the 4-milacre quadrats, shortleaf pine, the only true dominant, had a frequency of only 40 percent. Furthermore, the most characteristic understory tree, *Cornus florida,* counted on the same quadrats had a frequency of only 70 percent on the 4-milacre quadrat size. These two species, both characteristic of the type of community, showed frequency indices of 80 percent and 100 percent, respectively on the 25-milacre or largest quadrat. It was thought best, therefore, in spite of the increased labor, to use the 25-milacre quadrat size for the arborescent strata, since the true distribution of the characteristic trees in the stand is more accurately shown by this size than by that size designated by the species-area curve.

TABLE 1. RELATION BETWEEN TOTAL NUMBER OF SPECIES IN ARBORESCENT STRATA AND SIZE OF SAMPLE PLOT

Area Sampled (Milacres)	Quadrat Size (Milacres)	Number of Species	Percentage of total flora of the stratum	Percentage of total stand area
2.5	0.25	4	16	0.054
5	0.5	6	24	0.108
10	1	7	28	0.216
40	4	14	56	0.865
250	25	21	84	5.411
4,620	Total stand of 4.62 acres	25	100	100

TABLE 2. RELATION BETWEEN TOTAL NUMBER OF SPECIES IN THE SHRUB AND TRANSGRESSIVE STRATUM AND SIZE OF SAMPLE PLOT

Area Sampled (Milacres)	Quadrat Size (Milacres)	Number of Species	Percentage of total flora of stratum	Percentage of total stand area
2.5	0.25	22	37	0.054
5	0.5	28	48	0.108
10	1	31	53	0.216
40	4	39	67	0.865
4,620	Total stand of 4.62 acres	58	100	100

TABLE 3. RELATION BETWEEN TOTAL NUMBER OF SPECIES IN HERBACEOUS STRATUM AND SIZE OF SAMPLE PLOT

Area Sampled (Milacres)	Quadrat Size (Milacres)	Number of Species	Percentage of total flora of stratum	Percentage of total stand area
2.5	0.25	16	44	0.054
5	0.5	19	52.7	0.108
10	1	22	61	0.216
4,620	Total stand of 4.62 acres	36	100	100

The same thing, as regards the inadequacy of the species-area curve when used alone, held true for the shrubby and transgressive stratum. Probably the outstanding characteristic of this layer in the older stands is the great amount of oak reproduction. The frequency of all the species of transgressive oaks taken together is only 70 percent on the ½-milacre size at which this species-area curve breaks most strongly. This frequency, however, reaches 100 percent on the 4-milacre quadrat size. So, in order to give a more accurate picture of the developing hardwood reproduction, the 4-milacre size was adopted for the study of this stratum.

As a result of the preliminary investigation, ten of each of the three quadrat sizes selected were laid out in each of the stands except the abandoned field, in which 20 ¼-milacre plots were distributed. The quadrats were arranged in sets of three quadrats with the smaller sized plots being included within one corner of the largest plot. These sets were distributed as widely and evenly throughout the stands as was possible. They were laid out by means of tapes, usually in two rows of five sets each, although in some cases this procedure varied with irregularities in the outlines of the stand.

Because of the fact that the preliminary work was done on the basis of ten plots of each size, this number was employed for the surveys of the other stands. Knowledge of the number of quadrats to use would be very appropriate in a study of this kind. The results obtained with ten quadrats of large enough size and evenly distributed seem to be adequate, however, for this problem.

Individual counts of all the species concerned were made for each quadrat. The data were analyzed to determine frequency (Raunkiaer, 1918) and density (Braun-Blanquet and Pavillard, 1925) of each species in each stratum of every stand. Some of the density data were correlated statistically with certain soil factors by the method of Wallace and Snedecor (1931). For the herbaceous and shrubby flora, the nomenclature of Small (1933) was followed. Sudworth (1927) was followed in the synonomy of the arborescent species.

SOILS

IDENTIFICATION AND LOCATION OF PROFILES

The soil under the stands was examined first with an auger and then a trench or soil well was dug in each stand to the depth of the C horizon for the purpose of identifying the soil by its profile and texture. This was done before any vegetational work was begun.

The trenches were approximately 6 feet long and 18 inches wide and ranged in depth from 3 to 6 feet. Similar wells were dug in other parts of each stand. These were always placed 3 to 5 feet away from a dominant pine so that comparable root data could be obtained. The number of trenches in a stand varied, four being the number in each stand except the 13-year and

83-year old examples in which three were dug. Because of the much lower number of roots and the almost total absence of tree roots, two wells were thought to be sufficient for the abandoned field.

ROOT STUDIES

At the time the ditches were dug, the face nearest the tree was smoothed off and the horizons and roots mapped. This was done with the aid of a string grid with intervals of 6 inches. The profiles were mapped 4 feet horizontally and 3 feet vertically on the scale of an inch to a foot. The roots were grouped into the five following size classes: 0.01 to 0.1 inch, 0.11 to 0.3 inch, 0.31 to 0.5 inch, 0.51 to 1 inch, and those over 1 inch were measured individually. The root data were analyzed as to percentage of roots in each horizon and also as to the percentage of roots in successive 6-inch depths from the surface. The percentages of the various size classes in each horizon and at each depth were also determined. Average thicknesses of the horizons were obtained from nine measurements for each horizon in the profile. The measurements were taken at intervals of 6 inches along the vertical lines of the grid.

ANALYSIS AND MEASUREMENT OF PROPERTIES

A composite sample of two quarts of soil was taken from the whole length of each horizon in the profile and brought into the laboratory where the soil was spread out on paper until thoroughly air-dry. Before the soil was subjected to analysis, it was put through a 2 mm. sieve to remove pebbles and roots.

Mechanical analysis of at least one profile in each stand was made by a modification of the Bouyoucos (1927a, 1927b, and 1928) hydrometer method. On the basis of the data obtained, the horizons were assigned to textural grades following the classification of Davis and Bennett (1927).

The moisture equivalent of the soils was determined by the method recommended by Veihmeyer, Oserkowsky, and Tester (1928). A preliminary investigation of one profile in each stand showed that the lower horizons in all stands were essentially similar in moisture equivalent value. Therefore, only the A_1 and A_2 horizons and the dark layer denoting the depth of plowing in the younger stands were more intensively worked.

The carbon and organic matter contents of the soils were determined by a modification of Schollenberger's (1931) method. The method is based on the oxidation of the carbon with a standard solution of chromic acid in sulfuric acid. The excess chromic acid is titrated against a standard ferrous ammonium sulfate solution and the amount of chromic acid reduced is then calculated. From this is determined the amount of carbon necessary to reduce the given amount of the standard chromic acid. Carbon has been found to make up approximately 58 percent of the organic matter in the mineral horizons of soil (Russell, 1932), so the carbon content in percent multiplied

by the factor 1.724 equals the percentage of organic matter. Loss on ignition, as a measure of organic matter, was determined on the samples from one profile in each stand. Determinations were made for organic matter on samples from the A_1, "plowed", and A_2 horizons from every profile and on those from the B_1 from one profile in each stand.

Samples were taken in undisturbed condition adjoining each soil well for the determination of volume-weight (apparent specific density), water-holding capacity, and air capacity. These samples were taken in undisturbed condition by means of the brass ring sampler described by Coile (1936). A trench was dug alongside the soil wells to collect the samples from the middle of the A_2 and B_1 horizons. Samples of the first 2 inches of surface soil were taken about 10 feet from the soil wells to avoid soil which had been disturbed during the digging of the ditches. It was found that the surface soil samples would often not hold together when the ring was used in the steel sampler. This was overcome simply by pushing the brass ring into the soil with the foot until it was full, care being taken not to compact the soil. The samples were trimmed of excess soil in the field and each end of the brass ring fitted with a copper lid.

In the laboratory, both lids were removed and a filter paper and a copper screen placed over one end. The samples were then immersed in water for at least 24 hours. At the end of this time, one lid was replaced and the cylinder turned over under water and removed. Excess water was wiped off and the sample weighed immediately. The cylinder was then turned over and with the screened end down, allowed to drain on paper towels for one hour and then re-weighed. The difference between the first and second weighings is a measure of the apparent air capacity. After the second weighing, the sample was dried in an oven at 105° C. for 48 hours and then weighed for the oven-dry weight. The soil was removed from the cylinder and the cylinder, screen, lid, and filter paper weighed. It was found that the circle of filter paper held about 2 grams of water, therefore, 2 grams were added to the weight of the cylinder, screen, and paper in the wet condition. The water-holding capacity of the soil is calculated from the amount of water held in the soil at the time of the second weighing. Allowing 1 gram of water as equal to 1 c.c., this is expressed as percentage of total volume of the sample (600 c.c.). The weight per c.c. of this known volume of oven-dry soil is the apparent specific density or volume-weight.

The data obtained from the soil investigations were subjected to statistical analysis to determine their reliability. Any determination exceeding three times the standard deviation from the mean was rejected and a new mean computed. In only one case was it necessary to do this. Simple correlation coefficients were calculated among the soil factors during succession by the method of Wallace and Snedecor (1931).

RESULTS OF VEGETATIONAL ANALYSIS

The results of the statistical study of vegetation are assembled in Tables 4 to 8 and in Figures 5 to 10. The tables show the frequency and density of each species encountered in the various vegetational strata studied. No statistical study of the "Bodenschicht" or moss layer was made since mosses and lichens are very infrequent in the stands under consideration. The density referred to is the average number of stems of a given species per unit area (Braun-Blanquet and Pavillard, 1925). Cain (1932b) defines the concept as, "abundance on a unit area basis". Frequency is a measure of the uniformity with which the plants of a given species are distributed throughout the community (Raunkiaer, 1918). It is usually expressed as the "frequency index" or percentage of quadrats in which the species appears rooted of the total quadrats of that size in the stand.

Table 4 shows the density and frequency of woody dominants and subdominants which were counted on the largest size quadrats (25 milacres). Shortleaf pine, the principal dominant, has a very high density of 71.6 per 25 milacres or 2,864 stems per acre in the 9-year age class. Some idea of this crowded condition in the young stands may be gained from Figure 2. As shown in Figure 5, the density of this species in the arborescent stratum declines rapidly in the succeeding age classes and then gradually levels off to a density value of 1.5 per 25 milacres or 60 stems per acre in the 110-year old stand. A frequency of 100 percent is maintained by this species up through the 56-year age class; this falls off to 90 percent in the 83-year stand and to 80 percent in the oldest stand. This decrease in number of dominant

TABLE 4. DENSITY (D) AND FREQUENCY (F) OF WOODY DOMINANTS AND SUBDOMINANTS

Species		Stand Age						
		9	13	21	31	56	83	110
DOMINANTS								
Pinus echinata	d	71.6	50.6	30.9	12.8	6.3	3.8	1.5
	f	100	100	100	100	100	90	80
Pinus taeda	d	2.2	1.0	1.6	.8	.1	....	....
	f	90	60	80	70	10	....	....
Liquidambar styraciflua	d	.1	....	....	....	....	.2	....
	f	10	....	....	....	....	20	....
Diospyros virginiana	d	.2	....	....	....	....	....	....
	f	20	....	....	....	....	....	....
Juniperus virginiana	d	.4	....	....	....	....	....	....
	f	40	....	....	....	....	....	....
Liriodendron tulipifera	d	....	....	....	.1	....	....	....
	f	....	....	....	10	....	....	....
Quercus rubra	d	....	....	....	....	....	.1	....
	f	....	....	....	....	....	10	....
SUBDOMINANTS								
Liquidambar styraciflua	d	....	....	....	....	....	....	.3
	f	....	....	....	....	....	....	20
Oxydendrum arboreum	d	....	....	....	....	....	....	.1
	f	....	....	....	....	....	....	10

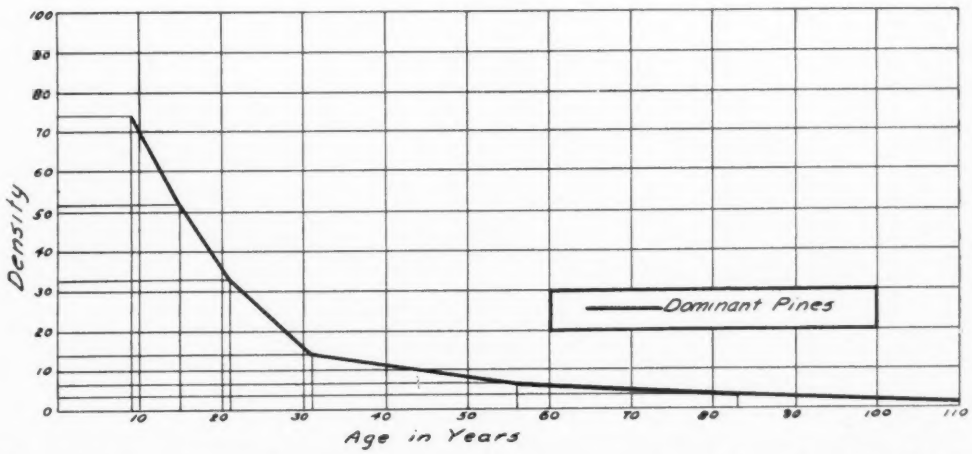

FIG. 5. Curve showing the decreasing density of the dominant pines from the 9-year stand to the 110-year stand. This curve is plotted from actual values.

stems and gradual opening of the stand is natural for a pure even-aged forest of pine which does not reproduce itself. The associated loblolly pine *(Pinus taeda)*, while never as dense as shortleaf pine, shows somewhat the same trend. It is almost negligible as a codominant after the stand is about 50 years old. The only other codominant found in more than one stand is sweet gum *(Liquidambar styraciflua)*. It seems occasionally to be an associate of the pine all through succession but in the stands studied, at least, is never very important. Red cedar *(Juniperus virginiana)* and persimmon *(Diospyros virginiana)* appear rather numerous as codominants in the 13-year stand but due to their slow growth, they are soon overtopped and never appear more important than secondary trees in older stands.

The secondary trees form a very definite layer society or synusia that becomes evident as the stand approaches middle age. In many stands it is quite distinct, especially in the spring when dogwood *(Cornus florida)*, redbud *(Cercis canadensis)*, and other conspicuous flowering trees are in bloom. Figure 9 shows this layer under an 85-year old pine canopy as it appears in early May with dogwood in bloom and other hardwoods coming into leaf. This stratum reaches a maximum height of about 35 feet but usually averages around 25 feet. Its flora is almost entirely broadleaved, the only exceptions being the two pine species, which soon disappear, and Juniperus which is fairly common all through succession. Dogwood is the most apparent species and also the one having the greatest density and frequency in this layer. It does not appear in any quantity or regularity as a secondary tree until the stand is between 40 and 50 years of age. From that time on, it is by far the most characteristic species in this layer. Two species occur in the secondary stratum in all stands. These are persimmon and tulip poplar *(Liriodendron tulipifera)*. The first shows no tendency to increase or decrease, merely holding its own, and never becomes more than 30 to 35 feet in height. The latter,

however, seems to be more numerous in older stands and it is possible that in some places, it might make up a part of the mixed deciduous forest which follows pine. Red maple *(Acer rubrum)* also seems to be quite important in older stands. It also shows a rather high amount of reproduction.

It is interesting to note that about middle age or between 50 and 60 years, several species of oaks begin to become important trees in the understory, this importance increasing in marked degree with increasing age of stand. Referring to Table 5, it can be seen that with the exception of tulip poplar, the oaks and hickories are the only potentially dominant genera which increase in number of individuals and also in extent of area covered through this particular type of succession.

Although the pine is still almost one hundred percent dominant in the mature stand, it is interesting to note in Figure 6 the comparison of the density and frequency of dominant and secondary hardwoods. As the density and frequency of the pines decrease, those values for the hardwoods increase, so that in the mature pine stand, the understory hardwoods have a density of over 13 times that of the pine and a frequency of 100 percent as compared with 80 percent for pine. It is very clear that as soon as one of the old dominant pines dies, the numerous hardwoods will quickly close the gap and the pine stand will be a step nearer the deciduous forest.

Probably the most interesting of the vegetational strata from the standpoint of succession is the shrub and "transgressive" layer. A detailed knowledge of reproduction in this stratum, coupled with an understanding of survival capacity of the various tree species, makes possible a fairly accurate prediction as to the future of the stand. The data concerning the secondary tree layer show to some extent survival capacity of an arborescent species. By combining the knowledge derived from this latter stratum with informa-

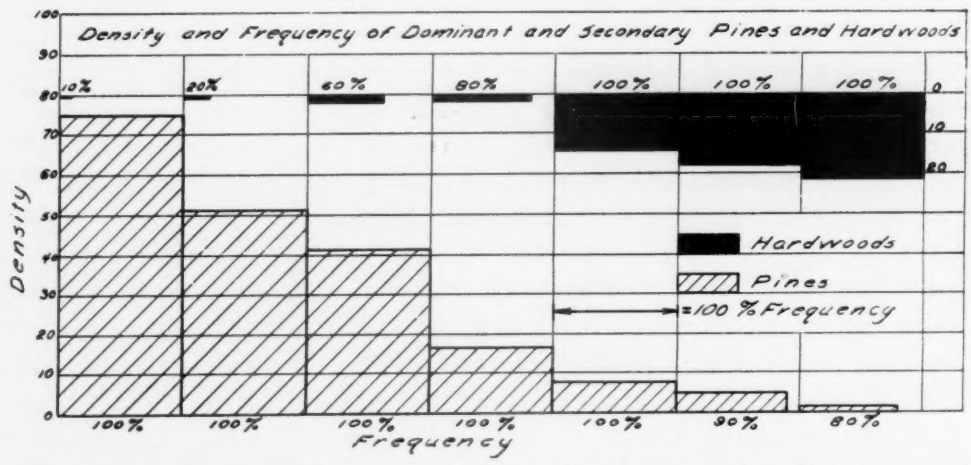

FIG. 6. The density and frequency of the dominant and secondary pines contrasted with the density and frequency of the dominant and secondary hardwoods throughout the succession. Note the increasing importance of the hardwoods and the steadily decreasing importance of the pines.

TABLE 5. DENSITY (D) AND FREQUENCY (F) OF SECONDARY TREES

Species		Stand Age				
		21	31	56	83	110
Pinus echinata	d	9.1	3.0	1.0	1.1	.1
	f	100	80	60	50	10
Pinus taeda	d	.1	.1	.1	....	....
	f	10	10	10	....	....
Diospyros virginiana	d	.2	.9	.1	.2	.2
	f	20	50	10	20	20
Liriodendron tulipifera	d	.5	.4	1.0	.8	2.0
	f	40	40	70	40	60
Platanus occidentalis	d	.1	....	....	....	....
	f	10	....	....	....	....
Sassafras variifolium	d	1.1	....	....	....	....
	f	20	....	....	....	....
Juniperus virginiana	d	....	.1	4.0	4.7	1.5
	f	....	10	90	90	90
Oxydendrum arboreum	d	....	.1	1.9	1.5	.9
	f	....	10	50	40	70
Acer rubrum	d	....	....	.8	.5	3.4
	f	....	....	40	40	50
Cornus florida	d	....	....	7.1	8.2	7.8
	f	....	....	100	100	100
Fraxinus americana	d	....	....	.1	....	....
	f	....	....	10	....	....
Hicoria glabra	d	....	....	.3	....	.4
	f	....	....	10	....	30
Liquidambar styraciflua	d	....	....	1.3	1.6	1.0
	f	....	....	60	80	50
Nyssa sylvatica	d	....	....	.2	.1	.2
	f	....	....	20	10	20
Ostrya virginiana	d	....	....	.1	.1	....
	f	....	....	10	10	....
Quercus alba	d	....	....	.1	....	1.6
	f	....	....	10	....	50
Quercus borealis var. *maxima*	d	....	....	.4	....	1.3
	f	....	....	20	....	60
Quercus velutina	d	....	....	.1	1.9	.8
	f	....	....	10	90	60
Ulmus alata	d	....	....	.1	.3	.1
	f	....	....	10	20	10
Viburnum rufidulum	d	....	....	.5	....	....
	f	....	....	40	....	....
Amelanchier canadensis	d	....	....	....	.1	....
	f	....	....	....	10	....
Cercis canadensis	d	....	....	....	.7	....
	f	....	....	....	30	....
Hicoria alba	d	....	....	....	.2	.5
	f	....	....	....	20	30
Quercus rubra	d	....	....	....	1.5	.4
	f	....	....	....	90	30
Quercus stellata	d	....	....	....	.4	....
	f	....	....	....	20	....
Styrax grandiflora	d	....	....	....	.1	....
	f	....	....	....	10	....
Ulmus americana	d	....	....	....	.1	.1
	f	....	....	....	10	10
Fraxinus pennsylvanica var. *lanceolata*	d	....	....	....	....	.1
	f	....	....	....	....	10
Fraxinus pennsylvanica	d	....	....	....	....	.1
	f	....	....	....	....	10
Morus rubra	d	....	....	....	....	.1
	f	....	....	....	....	10
Prunus serotina	d	....	....	....	....	.1
	f	....	....	....	....	10

tion concerning the amount of reproduction, it is possible to estimate the importance of a species as a future dominant.

The most striking feature in this lowest woody stratum is the rapid falling off and complete disappearance of shortleaf pine reproduction by the time the stand reaches 50 years of age. This is conclusive proof, when combined with the data on dominant and secondary pines, that the pine stage is ephemeral and eventually disappears because of its inability to reproduce under its own cover.

In sharp contrast to the amount of pine reproduction, is that of the hardwoods, especially the oaks. Figure 7 shows graphically the disappearance of

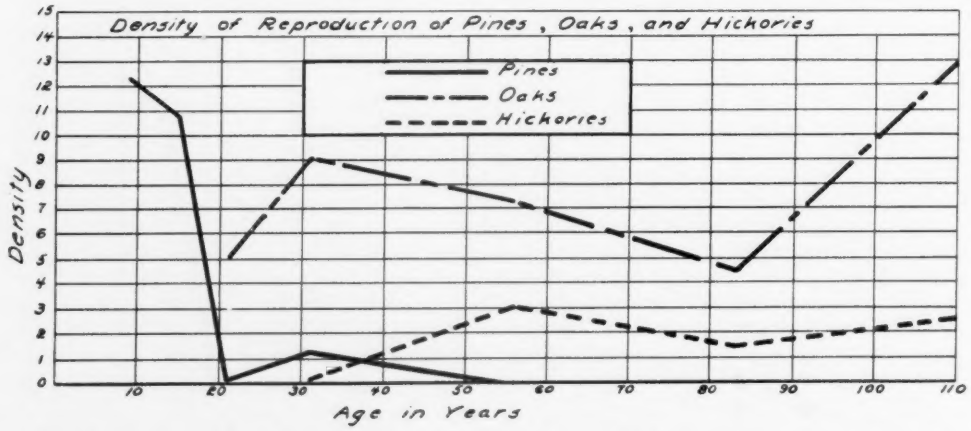

FIG. 7. Curves showing the density of pine, oak, and hickory reproduction throughout the succession. Note the disappearance of the pine reproduction and the increase in amount of oak and hickory reproduction.

the seedling pines and the sudden appearance and gradual increase of oak reproduction. The hickories enter shortly after the oaks and follow somewhat the same trend although they are nowhere as abundant as the latter. Combining this knowledge with what has been stated above concerning the abundance and frequence of oaks and hickories in the secondary layers of the older stands, it is safe to predict that in the deciduous community following shortleaf pine on these light-textured upland soils, these two genera will be foremost in importance. The species of oak most abundant in the younger stands is southern red oak *(Quercus rubra)*. It first makes its appearance as early as the 21-year stand and is very abundant both in that stand and in the 31-year stand. The other three species of oak *(Q. alba, Q. velutina,* and *Q. borealis* var. *maxima)* are much slower in becoming established. These three, however, all eventually become more abundant than *Q. rubra* in the oldest stand, with *Q. alba* being present in greatest numbers. These data show every indication that the eventual hardwood stand will approach the white oak-black oak-red oak cover type (Type 49) of the Society of American Foresters' Committee on Forest Types (1932).

The reproduction of red maple is interesting because of the fact that it is fairly abundant in every one of the pine stands and gradually increases in density with increasing age of stand. Its survival capacity under the pine cover is also good, as can be seen in Table 5. Because of its rapid development when grown in the open, it seems reasonable to predict that if the pine were cut, red maple would be one of the dominant trees in the hardwood stand immediately following cutting. However, in a stand which was not cut and the pines allowed to die out naturally, the more slowly growing oaks would have time to overtop the smaller red maple and the maple would remain as a secondary tree.

Among the other hardwoods, sweet gum *(Liquidambar styraciflua)*, which has fairly abundant reproduction in young stands, falls off in this respect in older stands and cannot be considered as a potentially important dominant following pine on these soils. The black gum *(Nyssa sylvatica)*, while nowhere very abundant, increases in both reproduction and in the secondary tree class with increasing age of the pine. This is probably due to a bettering of the moisture conditions since Nyssa tends to be a tree of moist places.

Dogwood, the tree showing the greatest amount of reproduction, is the most important tree of the secondary arborescent synusia. In the mature pine stand it shows a density of reproduction of 7,425 stems per acre and this combined with its 312 stems of secondary tree size per acre in the same stand, indicates the importance of this characteristic understory species. From the middle age classes of pine to maturity, it constantly increases its position as the most important secondary tree and it shows every indication of carrying this importance (as a secondary tree) over into the deciduous community. Observations on mature oak-hickory stands show that dogwood is apparently still the most characteristic understory tree and is still reproducing abundantly. As Lippmaa (1933) advocates and Cain (1934) suggests, this might be considered as an argument that, in some cases, layer societies or synusiae are separate communities in themselves being dependent on an overstory but entirely independent of the floristic composition of that overstudy. As Gleason (1936) has pointed out, this does not mean that such a synusia can be considered as a separate association because its individuals are in intimate association with the members of the other synusiae of the stand as regards the environmental factors. Thus, the stand is an intimate complex of several synusiae which may vary in themselves during the life of the stand or true association and if the association is successional, may even out-live the original association and become an integral part of its successor.

In the younger stands, the principal non-arborescent woody species is the trumpet vine *(Bignonia radicans)*. It is very abundant in some stands and entirely absent in others, but it seems never to be important in the oldest stands. A shrub characteristic of the pine forest is downy viburnum (*Viburnum rafinesquianum*). It appears very abundantly as soon as the crown cover is

TABLE 6. DENSITY (D) AND FREQUENCY (F) OF WOODY TRANSGRESSIVES IN SHRUB LAYER

Species		Stand Age						
		9	13	21	31	56	83	110
Pinus echinata	d	12.3	10.8	.2	1.3	....	....	....
	f	100	100	20	50	....	....	....
Pinus taeda	d	.2	....	.1	....	....	....	....
	f	20	....	10	....	....	....	....
Acer rubrum	d	1.8	.8	.5	2.1	2.3	2.0	9.4
	f	80	40	40	80	80	80	100
Cornus florida	d	.2	.5	.4	.5	13.3	13.4	29.7
	f	20	40	40	30	90	100	100
Juniperus virginiana	d	.3	.8	.2	1.1	2.5	3.1	.6
	f	30	70	20	50	70	90	40
Liquidambar styraciflua	d	6.8	3.1	....	.6	.2	3.3	.5
	f	90	80	....	20	20	80	20
Liriodendron tulipifera	d	.3	.7	.2	.9	.4	1.5	.5
	f	20	60	10	30	30	60	30
Oxydendrum arboreum	d	.1	....	.1	....	....	.2	1.0
	f	10	....	10	....	....	20	30
Platanus occidentalis	d	.1	....	....	....	....	....	....
	f	10	....	....	....	....	....	....
Ulmus alata	d	.2	.1	....	....	.1	.3	....
	f	20	10	....	....	10	10	....
Acer floridanum	d	....	.3	....	....	....	....	....
	f	....	20	....	....	....	....	....
Crataegus sp.	d	....	.1	....	.2	.1	....	.3
	f	....	10	....	10	10	....	20
Prunus angustifolia	d	....	.1	....	....	....	....	....
	f	....	10	....	....	....	....	....
Ulmus americana	d	....	.1	.2	....	....	....	....
	f	....	10	20	....	....	....	....
Viburnum rufidulum	d	....	.1	.1	.1	1.0	.1	.2
	f	....	10	10	10	60	10	10
Amelanchier canadensis	d	....	....	.1	.1	1.2	....	.7
	f	....	....	10	10	30	....	50
Celtis occidentalis	d	....	....	.1	....	.1	.1	....
	f	....	....	10	....	10	10	....
Juglans cinerea	d	....	....	.1	....	....	....	....
	f	....	....	10	....	....	....	....
Prunus pennsylvanica	d	....	....	.1	....	....	....	....
	f	....	....	10	....	....	....	....
Quercus alba	d	....	....	.2	.4	3.1	1.5	4.5
	f	....	....	10	40	90	70	100
Quercus phellos	d	....	....	.7	....	.2	.3	....
	f	....	....	20	....	20	30	....
Quercus rubra	d	....	....	4.0	7.8	2.5	1.5	2.7
	f	....	....	90	80	70	70	80
Quercus velutina	d	....	....	.2	1.5	1.1	1.1	2.9
	f	....	....	10	70	40	60	100
Sassafras variifolium	d	....	....	1.0	.7	2.5	.2	.8
	f	....	....	20	50	60	20	50
Ailanthus altissima	d	....	....	....	.1	....	....	....
	f	....	....	....	10	....	....	....
Diospyros virginiana	d	....	....	....	.5	.7	1.2	.8
	f	....	....	....	30	40	60	50
Hicoria alba	d	....	....	....	.2	1.5	1.4	.4
	f	....	....	....	20	50	70	30
Quercus borealis var. *maxima*	d	....	....	....	.4	.4	.1	2.9
	f	....	....	....	30	20	10	100
Fraxinus americana	d	....	....	....	....	1.1	....	....
	f	....	....	....	....	10	....	....
Hicoria cordiformis	d	....	....	....	....	.4	....	....
	f	....	....	....	....	40	....	....

TABLE 6. *(Continued)*

Species		Stand Age						
		9	13	21	31	56	83	110
Hicoria glabra	d	....	....	....	....	1.2	.1	2.2
	f	....	....	....	....	50	10	90
Nyssa sylvatica	d	....	....	....	....	.1	.5	3.0
	f	....	....	....	....	10	30	50
Ostrya virginiana	d	....	....	....	....	.1	.1	....
	f	....	....	....	....	10	10	....
Viburnum prunifolium	d	....	....	....	....	.2	.6	.2
	f	....	....	....	....	20	20	20
Cercis canadensis	d	....	....	....	....	....	.2	.3
	f	....	....	....	....	....	10	10
Morus rubra	d	....	....	....	....	....	.1	.1
	f	....	....	....	....	....	10	10
Quercus stellata	d	....	....	....	....	....	1.1	....
	f	....	....	....	....	....	30	....
Fagus grandifolia	d	....	....	....	....	....	....	.2
	f	....	....	....	....	....	....	10
Hicoria carolinae-septentrionalis	d	....	....	....	....	....	....	.2
	f	....	....	....	....	....	....	10
Ilex opaca	d	....	....	....	....	....	....	.2
	f	....	....	....	....	....	....	10
Prunus serotina	d	....	....	....	....	....	....	.2
	f	....	....	....	....	....	....	10

completely closed and is still fairly abundant in mature stands. Two woody vines, Virginia creeper *(Parthenocissus quinquefolia)* and muscadine grape *(Muscadinia rotundifolia)* form a very characteristic part of the shrubby flora of the older stands. Virginia creeper is present in the 9-year stand and becomes increasingly abundant as the pine reaches maturity. The muscadine grape, although not as abundant as Virginia creeper, shows an even more regular climb to its high density in the oldest stands.

As regards the herbaceous flora, the abandoned field is much richer than any of the pine stands. There is a gradual decrease in the number of herbaceous species until the crown is completely closed and from then on, the number of species remains fairly constant. However, Figure 8 shows that the herbaceous flora of the mature pine stand is almost entirely different floristically from that of the open field. Only two species, *Aster ericoides* and *Panicum sphaerocarpon,* are found in both locations. These are characteristic of the old field vegetation and occur in small openings in the mature stand.

The field vegetation is characterized by broom-sedge *(Andropogon virginicus)* and numerous other smaller species such as *Aristida dichotoma, Aster ericoides, Diodella teres, Plantago aristata, Lespedeza striata,* and *Juncus tenuis.* Broom-sedge is easily the dominant plant in this community (Figure 1) and grows in clumps uniformly distributed over the area. Most of the other species grow in the spaces between the clumps or in small open areas not yet occupied by broom-sedge. As pine comes in, this herbaceous

TABLE 7. DENSITY (D) AND FREQUENCY (F) OF SHRUBS AND WOODY VINES

Species		Stand Age						
		9	13	21	31	56	83	110
*Bignonia radicans	d	4.6	17.3	....	....	39.9	.1	.7
	f	20	30	....	....	90	10	30
Parthenocissus quinquefolia	d	.4	1.1	....	4.6	8.0	3.2	19.6
	f	20	20	....	90	80	90	80
Rubus cuneifolius	d	1.5	....	....	....	....	....	....
	f	10	....	....	....	....	....	....
Rubus flagellaris	d	.1	....	.4	.3	.3	....	....
	f	10	....	30	20	20	....	....
Polycodium neglectum	d	....	.1	.2	....	2.7	.4	10.6
	f	....	10	20	....	70	20	90
Toxicodendron toxicodendron	d	....	.1	2.0	....	3.3	.4	.3
	f	....	10	50	....	50	10	20
Ascyrum hypericoides	d	....	....	.1	....	....	....	....
	f	....	....	10	....	....	....	....
Benzoin aestivale	d	....	....	1.7	....	4.1	....	....
	f	....	....	40	....	70	....	....
Smilax bona-nox	d	....	....	.1	....	....	....	.4
	f	....	....	10	....	....	....	10
Smilax glauca	d	....	....	.9	.6	.1	.9	.9
	f	....	....	20	20	10	50	30
Smilax rotundifolia	d	....	....	.1	....	....	.3	3.3
	f	....	....	10	....	....	30	70
Cyanococcus vacillans	d	....	....	.1	....	....	....	....
	f	....	....	10	....	....	....	....
Viburnum rafinesquianum	d	....	....	4.3	1.6	4.9	5.8	2.1
	f	....	....	100	60	70	90	70
Muscadinia rotundifolia	d	....	....	.1	.7	.7	4.8	8.5
	f	....	....	10	20	20	60	30
Celastrus scandens	d	....	....	....	.1	....	....	....
	f	....	....	....	10	....	....	....
Nintooa japonica	d	....	....	....	2.9	.5	....	....
	f	....	....	....	20	10	....	....
Rosa virginiana	d	....	....	....	1.6	....	....	....
	f	....	....	....	10	....	....	....
Ceanothus americana	d	....	....	....	....	1.1	....	....
	f	....	....	....	....	10	....	....
Evonymus obovatus	d	....	....	....	....	.4	.9	....
	f	....	....	....	....	10	10	....
Ilex decidua	d	....	....	....	....	.1	....	....
	f	....	....	....	....	10	....	....
Phenianthus sempervirens	d	....	....	....	....	3.2	.9	1.8
	f	....	....	....	....	40	10	20
Rhus copal'inum	d	....	....	....	....	.1	....	.1
	f	....	....	....	....	10	....	10
Vitis aestivalis	d	....	....	....	....	.4	.5	.7
	f	....	....	....	....	20	30	50
Viburnum acerifolium	d	....	....	....	....	....	.8	....
	f	....	....	....	....	....	10	....
Cyanococcus corymbosus	d	....	....	....	....	....	....	1.7
	f	....	....	....	....	....	....	10

*In the old field Bignonia had a density of 33.6 based on a 4-milacre quadrat and a frequency index of 90.

vegetation falls off sharply in number of species and abundance of individuals and other species gradually replace those which disappear. In the middle-age classes of pine, the herbaceous flora is very sparse. This barren condition of the forest floor may be noted in Figure 3. Nevertheless, there are certain

TABLE 8. DENSITY (D) AND FREQUENCY (F) OF HERBS

Species		Old field	Stand Age 9	13	21	31	56	83	110
Acetosella acetosella	d	.6	4.9	....	....	....	....	....	....
	f	20	20	....	....	....	....	....	....
Agrostis alba	d	.25	.8	....	.2	.1	....	....	....
	f	20	40	....	20	10	....	....	....
Andropogon ternarius	d	.2	....	....	....	....	....	....	....
	f	20	....	....	....	....	....	....	....
Andropogon virginicus	d	13.65	.3	6.8	....	2.1	....	....	....
	f	100	30	50	....	60	....	....	....
Aristida dichotoma	d	7.85	....	....	....	....	....	....	....
	f	30	....	....	....	....	....	....	....
Aster dumosus	d	.05	....	....	....	....	....	....	....
	f	05	....	....	....	....	....	....	....
Aster ericoides	d	2.65	.2	.4	.8	1.7	....	....	.2
	f	100	10	30	20	40	....	....	10
Chamaecrista fasciculata	d	.75	.3	3.6	2.1	.1	.1	....	....
	f	50	30	80	90	10	10	....	....
Cyperus sp.	d	.45	....	....	....	....	....	....	....
	f	40	....	....	....	....	....	....	....
Diodella teres	d	6.4	.5	3.5	....	.1	....	....	....
	f	80	30	60	....	10	....	....	....
Erigeron ramosus	d	.15	....	....	....	....	....	....	....
	f	10	....	....	....	....	....	....	....
Gnaphalium obtusifolium	d	.2	.2	.5	....	.3	....	....	....
	f	20	20	40	....	10	....	....	....
Gnaphalium purpureum	d	.5	.8	1.3	....	....	....	....	....
	f	40	40	60	....	....	....	....	....
Gymnopogon ambiguus	d	.3	.2	1.8	2.7	....	....	....	....
	f	30	20	50	60	....	....	....	....
Helenium tenuifolium	d	.1	....	....	....	....	....	....	....
	f	10	....	....	....	....	....	....	....
Juncus tenuis	d	3.55	.2	.1	....	.1	....	....	....
	f	60	10	10	....	10	....	....	....
Kneiffia fruticosa	d	.05	.1	.1	....	....	....	....	....
	f	05	10	10	....	....	....	....	....
Lechea tenuifolia	d	.05	....	....	....	....	....	....	....
	f	05	....	....	....	....	....	....	....
Lespedeza striata	d	4.95	....	2.3	....	....	....	....	....
	f	80	....	10	....	....	....	....	....
Plantago aristata	d	8.65	....	....	....	....	....	....	....
	f	70	....	....	....	....	....	....	....
Polypremum procumbens	d	.25	....	....	....	....	....	....	....
	f	20	....	....	....	....	....	....	....
Potentilla canadensis	d	.3	....	....	....	1.1	....	.3	....
	f	10	....	....	....	50	....	20	....
Panicum sphaerocarpon	d	.3	....	....	....	1.7	.1	....	.3
	f	30	....	....	....	50	10	....	10
Sarothra gentianoides	d	.35	.2	....	....	....	....	....	....
	f	30	20	....	....	....	....	....	....
Scirpus sp.	d	.25	....	....	....	....	....	....	....
	f	10	....	....	....	....	....	....	....
Solidago altissima	d	.95	.7	....	....	....	....	....	....
	f	30	20	....	....	....	....	....	....
Solidago juncea	d	.15	....	2.2	....	.4	....	....	....
	f	15	....	40	....	30	....	....	....
Solidago nemoralis	d	.45	.1	1.2	....	.1	.1	....	....
	f	30	10	40	....	10	10	....	....
Specularia perfoliata	d	.1	....	....	....	....	....	....	....
	f	10	....	....	....	....	....	....	....
Strophostyles umbellata	d	.2	....	.1	.4	....	....	....	....
	f	20	....	10	30	....	....	....	....
Syntherisma sanguinale	d	.2	....	....	....	....	....	....	....
	f	20	....	....	....	....	....	....	....

TABLE 8. *(Continued)*

Species		Old field	Stand Age 9	13	21	31	56	83	110
Trifolium arvense	d	.3	.1	.2	....	....	....	....	....
	f	30	10	20	....	....	....	....	....
Ambrosia elatior	d	....	.2	.4	.1	....	....	....	....
	f	....	10	40	10	....	....	....	....
Asplenium platyneuron	d	....	.3	....	....	....	....	....	....
	f	....	10	....	....	....	....	....	....
Capriola dactylon	d	....	8.0	41.9	....	....	....	....	....
	f	....	20	100	....	....	....	....	....
Leucanthemum leucanthemum	d	....	.1	....	....	....	....	....	....
	f	....	10	....	....	....	....	....	....
Eupatorium capillifolium	d	....	.1	....	....	....	....	....	....
	f	....	10	....	....	....	....	....	....
Eupatorium hyssopifolium	d	....	.2	.2	.8	1.6	.2	....	....
	f	....	20	10	20	60	20	....	....
Falcata comosa	d	....	.1	....	....	.6	.4	.1	....
	f	....	10	....	....	30	30	10	....
Quamoclit coccinea	d	....	.4	.1	....	....	....	....	....
	f	....	10	10	....	....	....	....	....
Juncus setaceus	d	....	.3	....	....	....	....	....	....
	f	....	20	....	....	....	....	....	....
Panicum sp.	d	....	.1	....	....	....	....	....	....
	f	....	10	....	....	....	....	....	....
Passiflora incarnata	d	....	.2	....	....	....	....	....	....
	f	....	10	....	....	....	....	....	....
Physalis virginiana	d	....	.3	.7	.1	....	....	....	....
	f	....	10	30	10	....	....	....	....
Rynchosia erecta	d	....	.2	....	.4	.5	.6	....	....
	f	....	10	....	30	20	30	....	....
Tragia urens	d	....	.1	.4	....	....	....	....	....
	f	....	10	10	....	....	....	....	....
Martiusia mariana	d	....	....	.1	....	....	....	....	....
	f	....	....	10	....	....	....	....	....
Eragrostis pilosa	d	....	....	.3	....	.5	....	....	....
	f	....	....	20	....	30	....	....	....
Hieracium greenii	d	....	....	.6	....	....	....	....	....
	f	....	....	20	....	....	....	....	....
Lactuca sagittifolia	d	....	....	.1	....	....	....	....	....
	f	....	....	10	....	....	....	....	....
Meibomia arenicola	d	....	....	.6	.2	....	....	....	....
	f	....	....	20	10	....	....	....	....
Meibomia viridiflora	d	....	....	.9	....	....	....	....	....
	f	....	....	20	....	....	....	....	....
Xanthoxalis sp.	d	....	....	.3	....	....	....	....	....
	f	....	....	20	....	....	....	....	....
Andropogon sp.	d	....	....	....	.7	....	....	....	....
	f	....	....	....	50	....	....	....	....
Aster patens	d	....	....	....	.1	....	.3	....	....
	f	....	....	....	10	....	20	....	....
Chimaphila maculata	d	....	....	....	5.2	.4	2.0	.8	.2
	f	....	....	....	100	30	80	50	20
Crotalaria sagittalis	d	....	....	....	.1	.3	.1	....	....
	f	....	....	....	10	30	10	....	....
Lespedeza repens	d	....	....	....	1.0	.1	....	....	....
	f	....	....	....	20	10	....	....	....
Panicum ravenelii	d	....	....	....	.2	....	....	....	....
	f	....	....	....	10	....	....	....	....
Polygonatum biflorum	d	....	....	....	.1	....	....	.1	.1
	f	....	....	....	10	....	....	10	10
Biventraria variegata	d	....	....	....	....	.6	....	....	....
	f	....	....	....	....	50	....	....	....
Carex sp.	d	....	....	....	....	.1	....	....	....
	f	....	....	....	....	10	....	....	....

TABLE 8. *(Continued)*

Species		Old field	STAND AGE 9	13	21	31	56	83	110
Elephantopus tomentosus	d	....	....	....	....	.5	.5	2.4	2.2
	f	....	....	....	....	20	20	20	40
Aristolochia serpentaria	d	....	....	....	....	....	.2	.2	.3
	f	....	....	....	....	....	10	10	10
Cracca spicata	d	....	....	....	....	....	.2	....	....
	f	....	....	....	....	....	10	....	....
Galium sp.	d	....	....	....	....	....	.2	.1	.3
	f	....	....	....	....	....	20	10	30
Meibomia marylandica	d	....	....	....	....	....	.1	....	.7
	f	....	....	....	....	....	10	....	20
Ruellia ciliosa	d	....	....	....	....	....	.2	....	....
	f	....	....	....	....	....	10	....	....
Solidago boottii	d	....	....	....	....	....	.1	....	....
	f	....	....	....	....	....	10	....	....
Sorghastrum nutans	d	....	....	....	....	....	.1	.1	....
	f	....	....	....	....	....	10	10	....
Peramium pubescens	d	....	....	....	....	....	....	.7	....
	f	....	....	....	....	....	....	20	....
Tithymalopsis corollata	d	....	....	....	....	....	....	.5	.4
	f	....	....	....	....	....	....	30	30
Panicum boscii	d	....	....	....	....	....	....	.1	....
	f	....	....	....	....	....	....	10	....
Hexastylis virginica	d	....	....	....	....	....	....	....	.4
	f	....	....	....	....	....	....	....	10
Botrychium obliquum	d	....	....	....	....	....	....	....	.1
	f	....	....	....	....	....	....	....	10
Geum canadense	d	....	....	....	....	....	....	....	.1
	f	....	....	....	....	....	....	....	10
Gnaphalium sp.	d	....	....	....	....	....	....	....	.1
	f	....	....	....	....	....	....	....	10
Grass	d	....	....	....	....	....	....	....	1.0
	f	....	....	....	....	....	....	....	10
Potentilla pumila	d	....	....	....	....	....	....	....	.1
	f	....	....	....	....	....	....	....	10
Viola sp.	d	....	....	....	....	....	....	....	.7
	f	....	....	....	....	....	....	....	20

species which are typical of these age classes. These include *Chimaphila maculata, Eupatorium hyssopifolium,* and *Rynchosia erecta.* Slowly, the characteristic herbs of the mature stand become more numerous and species such as *Elephantopus tomentosus, Aristolochia serpentaria, Polygonatum biflorum, Tithymalopsis corollata,* and *Hexastylis virginica* become apparent. To what extent this flora continues on into the hardwood community is not known, but it is definite that some of the herbs such as Hexastylis and Polygonatum are found in some abundance in mature oak-hickory stands.

As a rough measure of the trend of homogeneity of the vegetation during succession, frequency graphs were employed. The frequency data were grouped into five classes as follows (Raunkiaer, 1918): Class A, those species appearing in from 1 to 20 percent of the quadrats of a given size in any one stand; Class B, those species appearing in from 21 to 40 percent of the quad-

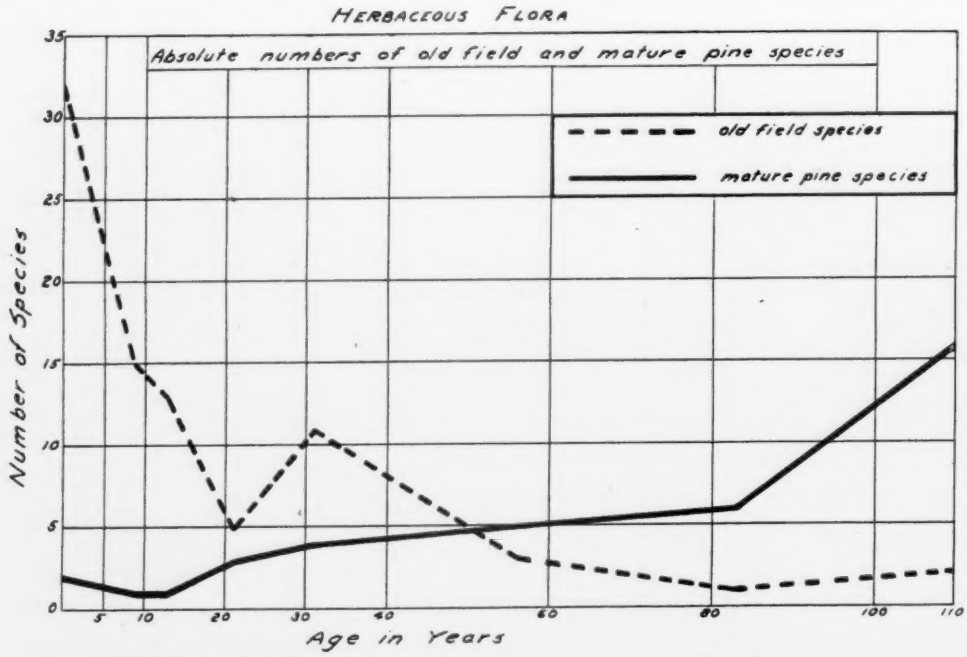

FIG. 8. The total number of old field herbaceous species throughout the succession contrasted with the total numbers of those herbaceous species which are present in the mature pine stand.

rats; Class C, those species appearing in from 41 to 60 percent of the quadrats; Class D, those species appearing in from 61 to 80 percent of the quadrats; and Class E, those species appearing in from 81 to 100 percent of the quadrats. Raunkiaer (1918), in summing up frequencies of over 8,000 examples, found that the species were distributed through the five classes as follows: Class A, 53 percent; Class B, 14 percent; Class C, 9 percent; Class D, 8 percent; and Class E, 16 percent. These percentages, when plotted, form a normal fishhook or J-shaped curve. According to Raunkiaer's "Law of Frequence", this curve results when analyzing the data from an association in a state of relative equilibrium. At this point, one or several species prosper at the expense of their neighbors and constitute the species to be found in the highest frequency classes. At the other end of the scale, many occasional and accidental species fill up Class A. The result, then, is a curve with a peak in Class A and another lower peak in Class E.

Series of graphs were constructed for each size of quadrat employed and also for the vegetation as a whole using the data from the different quadrat sizes. This latter would not ordinarily be possible since reliable graphs cannot be constructed from data obtained from quadrats which are not of a uniform size. However, in this case, different synusiae of the same association were sampled separately on special quadrat sizes so that no error is introduced and in combining the frequency data from the different synusiae a fair idea of the homogeneity of the vegetation of the entire phytocoenosis can be obtained.

FIG. 9. Stratification as illustrated in an 85-year old shortleaf pine stand. The secondary arborescent stratum is made up of *Cornus florida* (blooming), *Quercus*, and other hardwoods.

In Figure 10, the graphs for the ¼-milacre quadrats showing frequency indices of herbs are arranged in successional order. The striking fact exhibited by these curves is that, in the old field, the herbs form a fairly

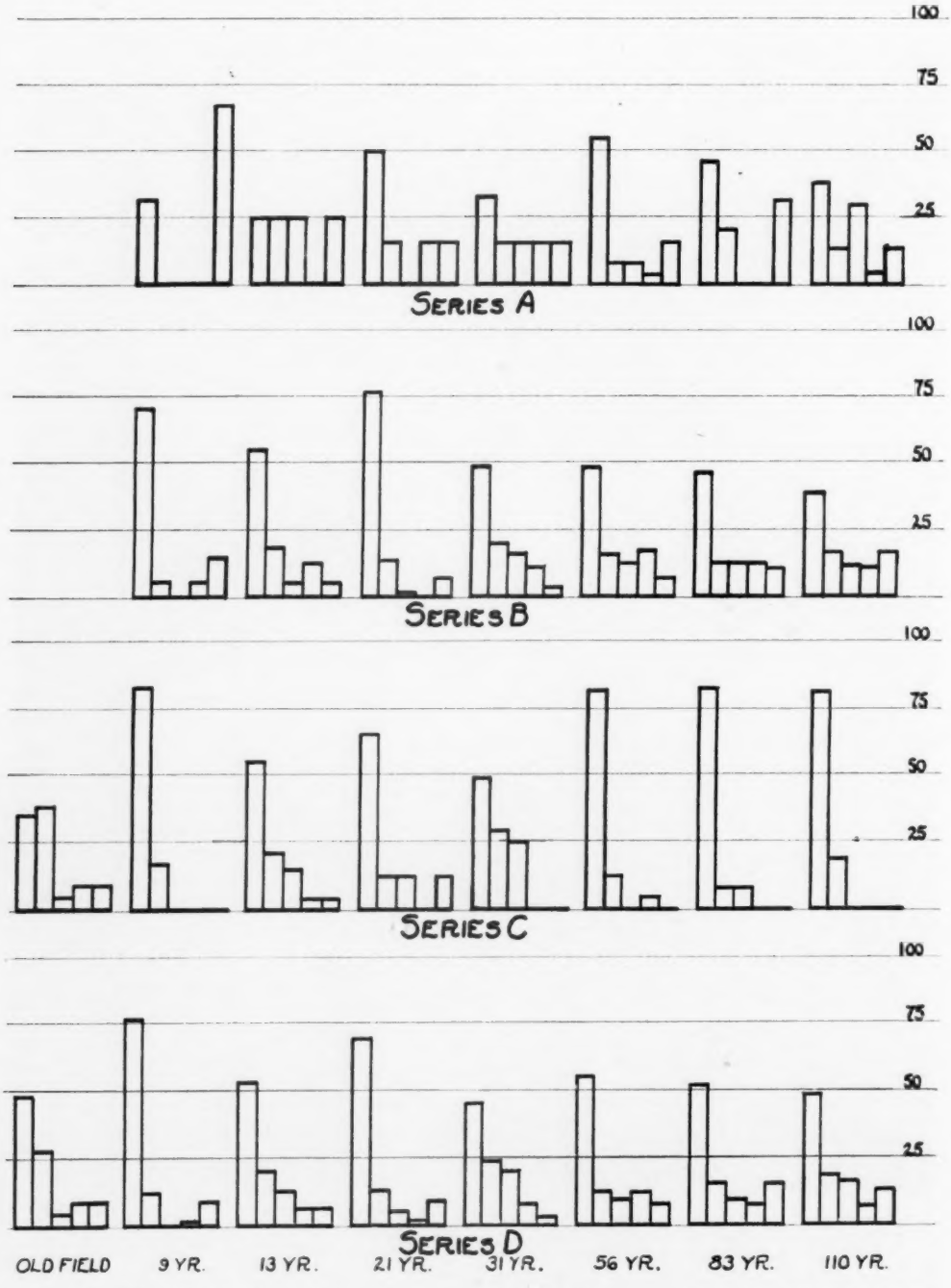

FIG. 10. The trend of the frequency curve through the succession as exhibited by the curves for the arborescent strata, the shrubby layer, the herbaceous layer, and the vegetation as a whole.

homogeneous community but as succession progresses, they become more and more scattered and less uniformly distributed throughout the association. This is indicated by the tendency of over 80 percent of the species to occur in the lowest frequency class in the oldest pine stands while few or none occur in the highest frequency classes in the same stands. Thus, the curves are very high in Class A and disappear entirely in Class E.

The vegetation of the shrubby layer shows a decided trend toward greater homogeneity as a stand approaches maturity. As is illustrated in Figure 10, the species of this stratum are at first mostly scattered throughout the stand but gradually become more evenly distributed and the result is a decrease in height of the peak in Class A and marked increases in the higher frequency classes. This same trend, though less pronounced, is followed by the species in the arborescent strata.

The lower series of curves in Figure 10 considers the vegetation as a whole. The abandoned field with its herbaceous vegetation is in a fairly homogeneous condition but this is considerably disturbed by the entrance of the pines as the frequency curve for the 9-year stand shows an unusually high peak in Class A, no species at all in Class C, and a low peak in Class E. As succession progresses, the vegetation becomes more homogeneous and the frequency curves for the oldest stands come remarkably close to Raunkiaer's normal denoting a close approach to a state of relative equilibrium.

RESULTS OF SOIL INVESTIGATIONS

COMPARABILITY OF THE STATIONS

THE PROFILE

The field data on the soil profile and also that on mechanical analysis show the succession to be worked out on inherently comparable light-textured lower Piedmont soils. The soil profile is characterized by a relatively thick (14 to 28 inches) A horizon of sandy loam underlain by a narrow (10 inches) B_1 horizon containing somewhat more clay and a relatively heavy B_2 horizon averaging about 15 inches in thickness. The almost unweathered C horizon extends to at least 8 feet in some instances.

The observed changes in the profile seem to be limited to the first few inches, so that a general description of the various horizons will suffice for all the stands. The A_2 horizon is a yellowish sandy loam of single grain structure which averages between 9 and 17 inches in thickness. The relatively narrow B_1 horizon is a friable, dull yellow sandy loam or sandy clay loam which is characterized by the presence of numerous black concretions about ¼-inch in diameter. This peculiarity of the B_1 horizon is found in every stand. The B_2 horizon is a compact, bright yellowish red sandy clay or clay. The C horizon underlying the B_2 horizon is a friable sandy clay or sandy clay loam. It is usually grayish in color, marked with splashes of red.

MECHANICAL ANALYSIS

In order to show that the soils in all the stands are similar in texture, the data from the mechanical analysis of one profile selected at random in each stand are given in Tables 9 to 14. Table 9, presenting the values for the surface of the mineral soil, shows that, in all the stands, the total sand content for this part of the profile is around 80 percent. The amount of clay ranges between 5 and 7.5 percent and tends to increase slightly in the older stands. This increase is undoubtedly due, for the most part, to the addition of organic colloids and not to any outstanding irregularities in the mineral soil, since the organic matter was not oxidized before mechanical analysis. According to the classification of Davis and Bennett (1927), the two oldest stands have a surface soil which is a sandy loam while all the other stands are on loamy sands. However, in all cases, the values for sands and clays come very close to the borderline between these textural grades. As far as the mineral soil is concerned, all the stands seem to be comparable.

In the younger stands, a cultural or "plowed" horizon was observed which had resulted from the mixing together of the surface soil during cultivation. This "plowed" horizon (Table 10) is very similar to the soil at the surface, being of the same textural grade. It has a sand content of from 80 to 82 percent and approximately 7 to 9 percent clay. With the exception of that in the 56-year stand, the A_2 horizons are all sandy loams ranging from approximately 73 percent to 78 percent sand content and from 9 to 14 percent clay content. The A_2 under the 56-year stand is a loamy sand with 82 percent sand and 7 percent clay. The mechanical analysis data for the A_2 horizon appear in Table 11.

The texture of the B_1 horizon is more variable. However, in all but two cases it is a sandy loam. These exceptions are a B_1 of sandy clay loam in the 9-year stand and a sandy clay B_1 in the 31-year stand. The percentages of the various size fractions in this horizon are included in Table 12.

The horizon having the greatest percentage of clay is the B_2. It is the most variable of the horizons, ranging from a sandy clay loam to a clay. It has its heaviest texture in the 31- and 110-year stands and is lightest in the old field. Table 13 shows the variation for this horizon among the stands.

The C horizon is more sandy than the B_2 and ranges from a sandy loam to a sandy clay. This horizon frequently contains veins of practically pure clay which are sometimes found as deep as 8 feet. Table 14 shows the percentage for the size classes in the C horizon.

From these data, it can be seen that the soil is sandy throughout the whole profile; yet it contains enough clay to provide a medium for base exchange and also enough to prevent excessive percolation of water. The texture of the upper three horizons in all the stands is very much alike. The texture of th B_2 horizon varies somewhat but scarcely enough to influence plant growth to any great extent, especially since only a very few roots extend as deeply

TABLE 9. MECHANICAL ANALYSIS* OF SURFACE SOIL

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	83.59	9.38	10.54	5.87	4.37
9 years	81.77	8.21	13.03	5.20	4.20
13 years	83.07	8.57	11.37	5.56	3.92
21 years	82.41	9.07	11.52	6.07	4.56
31 years	80.01	9.95	13.05	6.94	4.93
56 years	81.64	8.31	12.06	6.30	4.80
83 years	76.67	11.26	16.09	7.24	5.22
110 years	78.27	11.69	14.06	7.67	5.66

*The mechanical analyses are expressed in percentage.

TABLE 10. MECHANICAL ANALYSIS OF "PLOWED" HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	79.93	13.04	11.04	9.03	6.88
9 years	81.77	10.21	11.52	6.71	5.71
13 years	81.06	9.57	12.02	6.92	4.92
21 years	81.42	11.57	10.01	8.57	7.57

TABLE 11. MECHANICAL ANALYSIS OF A_2 HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	73.57	15.40	16.04	10.39	8.38
9 years	75.38	15.60	13.89	10.73	8.22
13 years	78.06	13.93	12.52	9.42	6.92
21 years	72.74	18.24	12.67	14.59	12.59
31 years	77.01	17.62	11.03	11.96	9.95
56 years	82.66	9.93	10.66	7.28	5.92
83 years	74.14	14.85	16.01	9.85	8.20
110 years	78.34	13.65	13.02	8.64	7.64

TABLE 12. MECHANICAL ANALYSIS OF B_1 HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	76.90	16.07	11.05	12.05	10.04
9 years	66.25	26.71	12.07	21.68	19.31
13 years	67.86	23.07	13.09	19.05	17.03
21 years	70.69	21.28	12.05	17.26	16.62
31 years	54.50	34.36	15.19	30.31	28.28
56 years	71.23	20.73	11.92	16.85	15.35
83 years	67.01	23.95	13.70	19.29	17.28
110 years	68.20	22.75	13.07	18.75	16.72

TABLE 13. MECHANICAL ANALYSIS OF B_2 HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	69.20	23.70	10.14	20.66	18.63
9 years	50.66	43.24	10.16	39.18	36.78
13 years	59.19	33.72	10.13	30.68	27.64
21 years	56.40	35.52	12.12	31.48	30.48
31 years	31.41	53.87	21.53	47.06	42.96
56 years	57.06	36.84	10.16	32.78	31.77
83 years	60.92	29.24	13.83	25.55	23.52
110 years	49.36	43.50	11.22	39.42	37.38

TABLE 14. MECHANICAL ANALYSIS OF C HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field*	.....	.....	.....	.....	.....
9 years	65.04	25.85	14.16	20.80	19.78
13 years	63.21	23.61	16.59	20.20	18.54
21 years	53.32	37.59	13.13	33.55	31.53
31 years	55.08	28.66	23.01	21.91	20.24
56 years	67.90	27.02	8.49	23.61	21.59
83 years	63.40	24.47	17.19	19.41	17.39
110 years	49.18	41.60	13.31	37.51	35.46

*No samples collected because of abnormal height of water-table at time of collection.

as this horizon. The one effect of the heavier B horizons would be in slowing down percolation so that these stands would remain moist for a longer time in the spring. During the growing season, however, such a heavy B_2 horizon would have very little effect on the moisture relations of plant and soil, since the summer rains seldom penetrate deeper than a few inches.

CHANGES

EVOLUTION OF THE PROFILE

That there is a distinct change in the upper part of the soil profile, is evident from Figure 11. This figure shows the development of the soil profile during its 110-year occupancy by the pine, plotted from the average thicknesses of the mineral and organic horizons in each stand.

In the abandoned field, there is, at the top of the mineral profile, a layer, almost 12 inches thick, which is dark yellowish brown in color. This layer or horizon is very homogeneous and is the visible effect of cultivation. Hence, it will be referred to as the "plowed" horizon. The organic horizons are practically absent in the old field, there being only a very little herbaceous litter.

In the 9- and 13-year old pine stands, the "plowed" horizon is thinner than that in the old field, being little over 6 inches thick. In these same stands, there is a marked increase in the thickness of the litter and the appearance of a fermentation layer of partially decayed needles.

Progressing to the 21-year age class, it is seen that the *brown* "plowed" horizon is overlain with a very thin (0.5 inch) *blackish gray* A_1 horizon. The "plowed" layer has gradually become thinner and the distinctly different colored A_1 horizon develops over it and eventually replaces it. The total thickness of the organic horizons in this stand is about 1½ inches. The humus layer is still absent.

In the 31-year stand, the "plowed" horizon has completely disappeared and the blackish gray A_1 horizon has become almost 3 inches thick. The total thickness of the organic horizons in this stand is not as great as that in the 21-year stand but it is marked by the first appearance of a humus layer, in addition to the litter and fermentation layers.

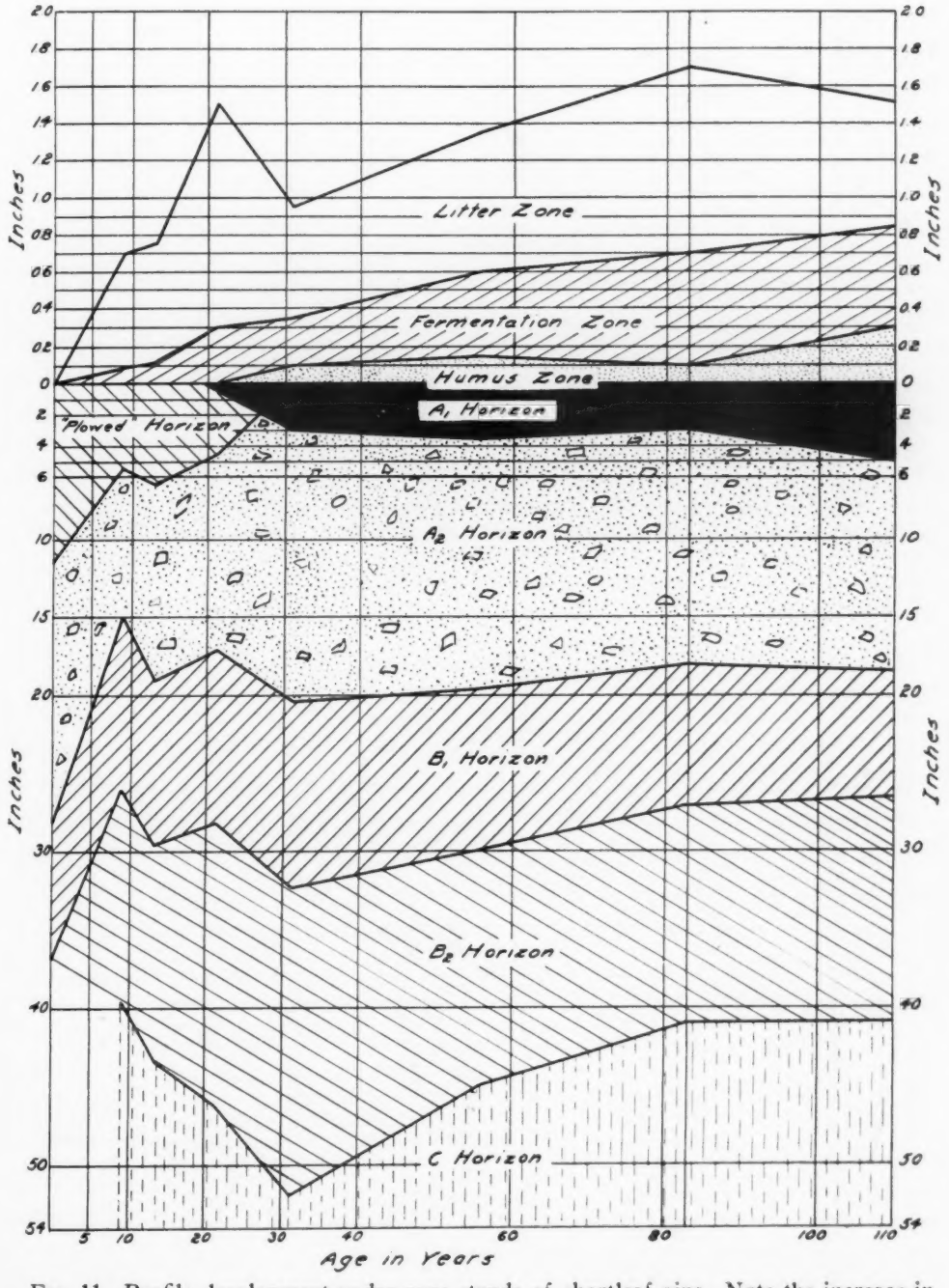

FIG. 11. Profile development under pure stands of shortleaf pine. Note the increase in depth of the organic horizons and the gradual replacement of the "plowed" horizon by the A_1 horizon.

From the 31-year stand to the 110-year stand, the general trend of the profile development is toward a thicker A_1 horizon which gradually acquires a good crumb structure through the addition of organic matter and the activity of soil fauna. The organic horizons tend to increase in total thickness,

seldom, however, becoming much over 1½ inches deep. Both the fermentation and the humus layers show marked increases in thickness but the litter remains more nearly constant. The profile under the pine, then, has the appearance of a podsolic soil with some organic accumulation on the surface, a dark A_1 horizon, a bleached or light-colored A_2 horizon, and a zone of accumulation in the B horizons.

ORGANIC MATTER

The results obtained by the wet combustion method for the determination of organic matter are presented in Table 15. These results for the surface

TABLE 15. AVERAGE ORGANIC MATTER CONTENTS BY THE WET COMBUSTION METHOD
(Percentage of oven-dry weight)

Stand	Surface	"Plowed"	A_2	B_1
Old field	0.852	0.706	0.190	0.193
9 years	0.823	0.487	0.198	0.175
13 years	0.707	0.437	0.147	0.070
21 years	1.328	0.684	0.328	0.331
31 years	1.649	.....	0.451	0.2206
56 years	1.792	.....	0.275	0.179
83 years	2.795	.....	0.371	0.206
110 years	2.944	.....	0.474	0.215

soil and the A_2 horizon are shown graphically in Figure 12 as are also the values for the same horizons obtained by the ignition method. The surface soil shows a marked trend toward increased organic matter content with increased age of stand. The surface soil of the abandoned field and the younger stands shows less than 1 percent organic matter by the wet combustion method while that of the mature pine stand shows almost 3 percent organic

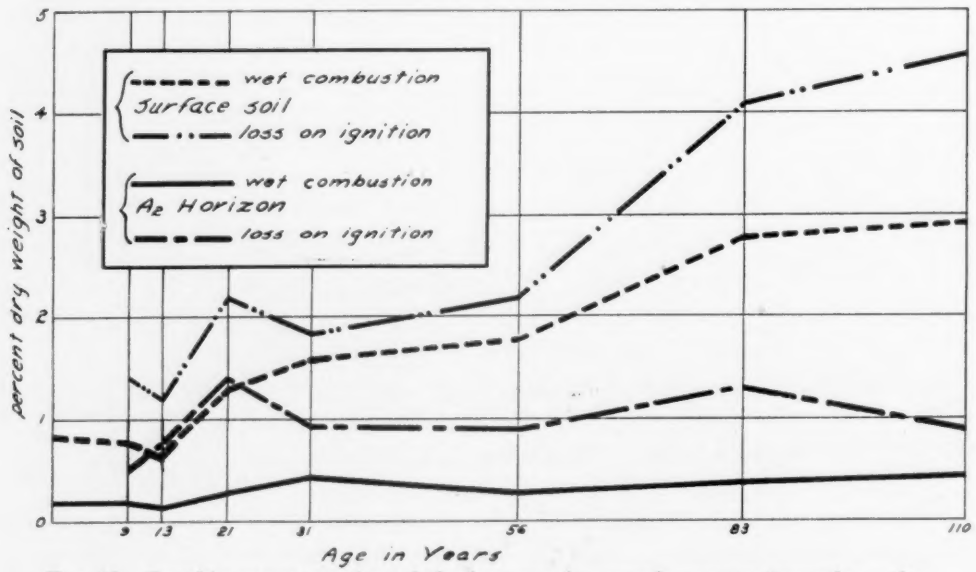

FIG. 12. Graphic representation of the increase in organic matter throughout the shortleaf pine succession.

matter by the same method. The amount of organic matter is low in the A_2 and is still lower in the B_1. There is a slight tendency toward increase in organic matter with age in both these horizons. The values obtained from loss on ignition run higher in every case than those obtained by the wet combustion method due to the driving off of the bound water and the water of hydration in the colloids.

MOISTURE EQUIVALENT

The data shown in Table 16 are the average moisture equivalents for the different horizons through the pine succession. Since the moisture equivalent is a function of the amount of colloidal material in the soil, it would be expected to increase with an increase in colloidal content. Although the texture of the surface soil is essentially the same in all stands of the successional series, the moisture equivalent increases due to the previously mentioned in-

TABLE 16. AVERAGE MOISTURE EQUIVALENTS

Stand	Surface	"Plowed"	A_2	B_1	B_2	C
Old field	6.84	8.32	8.14	10.015	17.17	.....
9 years	6.45	6.67	7.40	15.07	28.00	20.12
13 years	6.06	6.22	7.31	13.29	20.30	20.18
21 years	7.20	6.80	9.71	13.29	22.21	25.31
31 years	7.685	....	8.24	17.26	28.70	24.03
56 years	7.33	....	7.08	14.49	28.14	17.89
83 years	11.52	....	9.31	13.81	20.75	20.18
110 years	10.43	....	7.29	14.92	26.87	25.54

creases in the amount of organic matter. This is substantiated by the highly significant correlation coefficient of 0.949 obtained between organic matter content and moisture equivalent of the surface soil through this succession.

In the younger stands, the surface soil has a lower moisture equivalent than the A_2 horizon because of the former's inherently lower content of inorganic colloids. However, in the older stands, the moisture equivalent of the surface soil is higher than that of the A_2 horizon. The surface soil in the older stands is still below the A_2 in total "colloidal" content as determined by a hydrometer, but it has a higher moisture equivalent because of the addition of organic colloids which are much more hygroscopic than inorganic colloids. As would be expected, the horizons having the greater amounts of clay have the higher moisture equivalents. The B_2 horizon, in general, shows the highest values of the profile, these values ranging between 20 and 29 percent. These results show that the only change in moisture equivalent during pine succession is an increase in the A_1 horizon due to the increase in the amount of organic colloids in that horizon.

VOLUME-WEIGHT

The volume-weight or apparent specific density of soils is a measure of compactness. These results are presented in the form of averages in Table 17.

TABLE 17. AVERAGE VOLUME-WEIGHTS

Stand	Surface	A_2	B_1
Old field	1.346	1.749	.....
9 years	1.329	1.541	1.915
13 years	1.346	1.558	1.687
21 years	1.265	1.508	1.624
31 years	1.210	1.653	1.606
56 years	1.123	1.561	1.787
83 years	1.143	1.556	1.834
110 years	1.029	1.520	1.756

The surface soil is shown to be relatively porous as compared to the rest of the profile and that compactness increases with depth, at least to a certain point. There is a marked decrease in the volume-weight of the surface soil through succession from a value of 1.346 in the abandoned field to 1.029 in the mature pine stand. This same trend is shown to a lesser degree in the A_2 horizon. A highly significant correlation coefficient of —0.911 between organic matter and volume-weight in the surface soil shows that the volume-weight of the A_1 horizon is strongly associated with the organic matter content of that horizon. An increase in the amount of organic matter is accompanied by a decrease in the volume-weight. This increased porosity and lighter weight of the surface soil through succession might therefore be said to be due to increased organic matter and its attendant phenomena, presence of root channels, activities of soil fauna, and crumb structure.

TABLE 18. AVERAGE WATER-HOLDING CAPACITIES

Stand	Surface	A_2	B_1
Old field	33.705	27.084	.....
9 years	36.177	30.662	25.496
13 years	36.038	30.775	33.222
21 years	42.400	37.206	33.500
31 years	40.469	27.761	33.790
56 years	41.482	28.360	28.440
83 years	43.485	30.077	26.273
110 years	45.274	31.731	30.968

TABLE 19. AVERAGE AIR CAPACITIES

Stand	Surface	A_2	B_1
Old field	7.733	4.122	.....
9 years	7.607	7.538	4.943
13 years	7.899	6.399	6.553
21 years	6.094	4.940	4.386
31 years	9.093	5.038	5.706
56 years	12.738	5.210	4.050
83 years	8.135	4.606	2.883
110 years	8.363	5.705	3.663

WATER-HOLDING CAPACITY

The ability of the soil mass to hold water against the pull of gravity is known as the water-holding capacity (the "Wasserkapazitat" of the German and Swiss workers). It is here expressed on a volume basis as the amount of water held per unit volume. The averages of the water-holding capacity determinations are recorded in Table 18. The averages show that to a certain point, at least, the water-holding capacity decreases with depth. Of the three horizons sampled, the surface soil, in general, has much higher values than the A_2 and B_1 horizons. No water-holding capacity determinations were made for the B_2 horizon but such determinations would probably show higher values because of the higher clay content. The only marked tendency to change under the influence of pine is exhibited by the surface soil which shows an increase from a value of 33.705 percent volume in the abandoned field to a value of 45.274 percent volume in the mature stand. This increase is due almost entirely to the addition of organic matter as is brought out by the highly significant correlation coefficient of 0.884 obtained between these two factors in the surface soil through succession. A high correlation of 0.930 was also obtained between average total thickness of the organic horizons and the water-holding capacity of the A_1 horizon. The highly significant inverse correlation of —0.840 between water-holding capacity and volume-weight in the same horizon shows the dependency of the two on the factor of organic matter and to some extent on each other.

AIR CAPACITY

The data on air capacity show no definite trend toward an increase or a decrease in this factor throughout the pine succession. Aichinger and Siegrist (1930) have shown that there is an increase in the air capacity during an alder succession on the sandy soils in central Europe. Since there is no consistent increase in this instance, it may be that more samples taken in the older stands would yield better results. As would be expected, the surface soil has the greatest air capacity ranging from 8.094 percent by volume in the 21-year stand to 12.738 percent by volume in the 56-year stand. The data, in the form of averages, are presented in Table 19.

RESULTS OF ROOT STUDIES

It is very evident from Table 20 that there is scarcely any change in the total number of roots in the whole profile after the pines have become estab-

TABLE 20. AVERAGE NUMBER OF ROOTS PER 12 SQUARE FEET OF PROFILE IN EACH STAND

Old field	114.
9-year stand	262.2
13-year stand	285.6
21-year stand	276.5
31-year stand	224.75
56-year stand	247.
83-year stand	220.
110-year stand	307.5

lished. With the closing of the crown canopy, there seems also to be a closing of the root network. During the pine dominance, at least, this network seems to be fairly constant in the total number of roots of which it is composed.

Probably the most striking feature brought out by the root studies is the fact that in all the stands most of the roots are in the upper 6 inches of mineral soil. Table 21 shows the percentage of the total roots in the profile

TABLE 21. DISTRIBUTION OF TOTAL ROOTS IN SUCCESSIVE 6-INCH DEPTHS (Percentages)

Age of stand	1st 6 in.	2nd 6 in.	3rd 6 in.	4th 6 in.	5th 6 in.	6th 6 in.
Old field	95.61	4.39	....	....	....	....
9 years	62.45	21.83	7.81	4.48	2.66	1.76
13 years	61.83	24.85	6.16	4.20	1.61	1.15
21 years	55.78	19.89	15.91	4.70	2.44	1.26
31 years	62.82	16.57	9.34	4.56	5.22	1.44
56 years	60.82	21.25	9.41	4.35	2.93	1.21
83 years	63.18	17.27	11.36	4.36	2.86	.90
110 years	64.14	16.82	7.80	2.60	4.71	3.90

which are found in successive 6-inch depths. In the abandoned field, populated with shallow-rooted herbs, over 95 percent of the roots are in the first 6 inches and the remainder are in the second 6 inches. With the entrance of the pines and other woody species, deeper pentrating roots appear and the percentage of total roots of the profile in the first 6 inches falls to a little over 60 percent. Here again an equilibrium seems to be established with the closing of the crown canopy since there are no significant changes in the concentration of roots in the different depths until the stand is mature. In the mature pine stand, there is a slightly higher number of roots at the deeper depths. This may be a result of the better utilization of the soil by the deeper rooted species which enter late in the pine stage. Again, it may be the result of the slightly higher colloidal content in the lower part of the 3-foot section in the oldest stand.

Since most of the roots are in the upper 6 inches of soil, it would be expected that the soil horizons in that zone would contain higher percentages of the total roots than would the deeper horizons. This is shown to be the case in Table 22. The "plowed" horizon up through the 21-year old stand con-

TABLE 22. DISTRIBUTION OF TOTAL ROOTS THROUGH THE VARIOUS HORIZONS (Percentages)

Stand	A_1	P_L	A_2	B_1	B_2	C
Old field	.....	98.24	1.76	....	....	....
9 years	.....	59.84	27.65	6.19	5.72	.57
13 years	.....	70.58	22.96	4.65	1.75	....
21 years	2.16	47.19	43.12	6.05	1.44	....
31 years	34.48	.....	55.28	8.12	2.11	....
56 years	42.20	.....	48.98	6.57	2.22	....
83 years	37.72	.....	53.77	6.36	2.09	....
110 years	60.73	.....	26.66	4.79	7.80	....

tains the greater part of the roots of the profile. The A_1 horizon, as it grows thicker, contains an increasing percentage of the total roots. It is only in the oldest pine stand, though, that it contains more roots than the A_2 horizon. However, the A_1 horizon is always thinner than the A_2 and contains more roots per unit area of profile exposed than does the latter. Tamm (1920), in Sweden, found that roots tended to avoid the light-colored A_2 horizon. In the stands considered in the present study, however, this is not the case. They are not as abundant per unit area in the A_2 horizon but there seems to be no indication of an avoidance of this area by roots. This conforms with the findings of Hesselman (1910) in northern Sweden and Laitakari (1929) in Finland, both of whom worked with Scotch pine *(Pinus sylvestris)* on sandy soils. In all the stands in the present study, less than 13 percent of the total roots occurred in the B horizons.

The percentages of the various size classes of roots in each stand are presented in Table 23. In all but one stand, over 80 percent of the roots range

TABLE 23. DISTRIBUTION OF TOTAL ROOTS IN THE VARIOUS SIZE CLASSES (Percentages)

Stand	0.01-0.1 in.	0.11-0.3 in.	0.31-0.5 in.	0.51-1 in.	Over 1 in.
Old field	100	.....	.....	.....	.....
9 years	92.75	5.91	1.14	0.19	.....
13 years	86.48	11.55	1.15	0.70	.10
21 years	86.16	10.84	1.89	0.99	.09
31 years	83.20	13.45	2.22	0.89	.22
56 years	85.02	10.62	1.82	1.92	.60
83 years	79.36	13.63	3.00	2.27	1.63
110 years	85.36	9.67	2.43	1.54	.97

from 0.01 to 0.1 inch in diameter. Here also there seems to be an equilibrium established with the closing of the root network. In the old field, all the roots are of this smallest size class. In the 9-year stand, the percentage of the smallest roots falls to approximately 93 percent and in the 13-year stand to approximately 86 percent, after which the percentage remains practically constant all through the pine succession. The only other change of any significance, as regards size of roots, is the increase in number of larger roots in the older stands. This, of course, is the natural result of the increase in size of the trees.

To show the locations and numbers of the various sized roots in the profiles of three representative stands, Figures 13 to 15 have been constructed from the average number of roots of each size class in successive 6-inch depths. These figures show graphically the fact that most of the roots are in the upper 6 inches of the soil. They also show that the smaller roots are relatively more numerous in the first 6 inches than they are in the second 6 inches, because of the fact that many of the larger roots are found between the 6- and 18-inch depths while the smaller roots are located closer to the

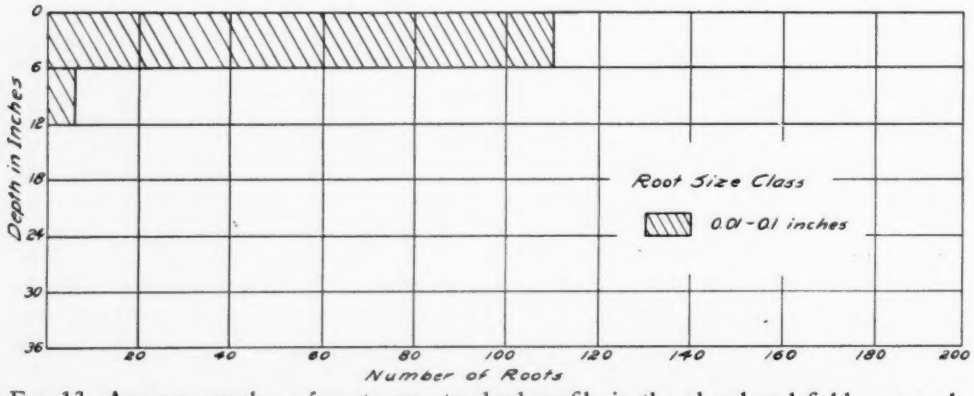

FIG. 13. Average number of roots per standard profile in the abandoned field arranged according to depth and size class.

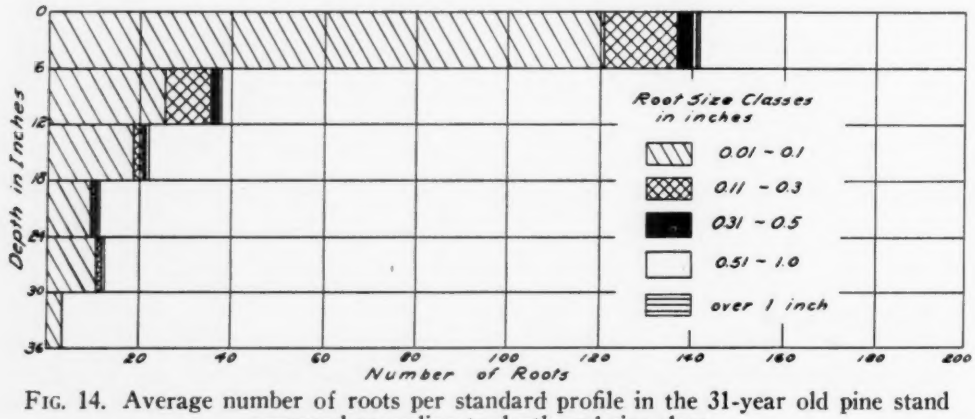

FIG. 14. Average number of roots per standard profile in the 31-year old pine stand arranged according to depth and size class.

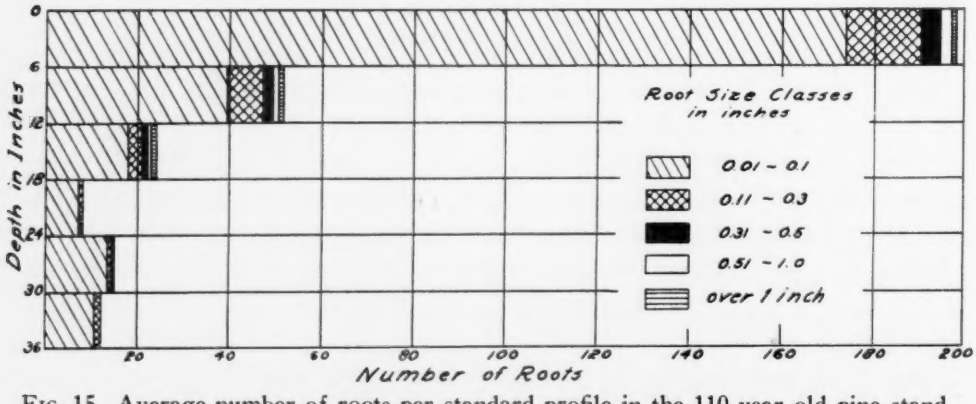

FIG. 15. Average number of roots per standard profile in the 110-year old pine stand arranged according to depth and size class.

surface. The tendency of roots to penetrate more deeply in the older stands is also apparent from the diagrams.

These same data arranged on a horizon basis are not included in tabular or graphic form. It will suffice to say that in practically every case, the "plowed" and A_1 horizons show the great numbers of the smallest size class

only and that the greatest numbers of all the larger size classes are in the A_2 horizon. Most of the roots in the B horizons are very small, although occasionally larger ones are present, especially in the older stands.

CORRELATION AND INTEGRATION

In any analysis of plant succession, many factors must be considered. The slow but constant change, both in the vegetation and the environment, cannot be completely interpreted in terms of any one factor. It is, rather, a complex of factors which is both the cause and effect of change. Because of the delicate balance between the factors of the environment, it is impossible for one factor to change without affecting others and these, in turn, may affect still others. Thus, the environmental complex itself is subject to change at the slightest stimulus and the result is far-reaching readjustments within the whole organismo-environmental system. Early in succession, the complex is especially unstable and consequently there are rapid changes as revealed by constant readjustments in the vegetation and the soil. Later, through the approaching of equilibria among some of the factors, there is a gradual retardation of change, the decrease continuing to a condition of near-stability. This state of near-stability, which is never absolute, is commonly known as the climax condition.

It has been the purpose of this study to determine certain of these changes in the vegetation and the soil during the early stages of forest succession and to attempt to evaluate and integrate them. By delimiting the work to areas essentially comparable in topography, climate, and soils, it has been possible to study the mutual effects of the vegetation and the physical properties of the soil during succession and the changes in the organismo-environmental complex produced by these mutual effects.

The virgin deciduous forests which occupied these areas of light-textured Lower Piedmont soils at the time of the coming of the white man were probably in the near-stable climax condition. They were climax not only as regards vegetation but also as to soil which was mature with well-developed horizons. Cain (1932a) has shown the virgin deciduous forest to be uneven-aged and composed of all sizes of trees surrounded by abundant reproduction. In the constant competition for water, light, and the other necessities of life, only that reproduction survives which is physiologically and morphologically able to withstand adverse conditions until the death of a tree in the overstory releases it from suppression and allows it to take its place in the arborescent strata. Auten (1933) has demonstrated that the effect of such a virgin hardwood forest on the soil is to make it porous and water-absorbent through the effects of organic matter, soil fauna, and root channels. When a forest is cut off, the equilibrium of the factor complex is greatly disturbed. The porous, light forest soil is cultivated and mixed by the plow and, because of the absence of protective litter, is puddled by the impact of rain and a hard,

relatively impermeable crust is formed. The organic matter in the soil is subject to rapid oxidation, the soil fauna changes or disappears, and the result is a single-grained, relatively non-porous soil which has little resemblance to the highly developed forest soil.

It is in this degenerate state that the soil is turned back to nature. The typical abandoned field habitat is characterized by its exposure to direct sunlight and its poor physical soil conditions. These latter include low porosity, low water-holding capacity, and low absorptive power. All of these are more or less the result of the absence of organic matter and a plant covering. The effects of cultivation are still apparent in the well-defined furrows and the presence of the brown homogenous "plowed" zone at the top of the profile.

The first seed plants to invade this bare area are annuals such as *Syntherisma sanguinale, Sarothra gentianoides,* and *Leptilon canadense.* These enter during the first year after abandonment and are largely replaced during the second year by the annual *Ambrosia elatior* and the perennial *Aster ericoides.* Such an outstanding change in the vegetation within one year is an illustration of the previously pointed out unstable condition of the organismo-environmental complex in the early stages of secondary succession. Gradually, in the third and fourth years after the last cultivation, the annuals are replaced by perennials such as *Andropogon virginicus, Eupatorium hyssopifolium, Eupatorium capillifolium,* and several species of Solidago. The roots of these plants are able to penetrate the relatively compact surface soil and because of their perennial habit, can persist indefinitely when once established. Their roots seldom penetrate deeper than 10 inches and occur almost entirely in the brown "plowed" zone. Comparatively few roots are present in the herbaceous stage of dominance and, obviously, because of incomplete utilization of the soil by these roots, the habitat is not closed to further invasion. Simple correlation data between total thickness of the organic horizons and number of old field herbaceous species present through succession shows the highly significant figure of —0.973. Such a value denotes a high inverse correlation between number of these old field species and accumulation of organic debris. This inverse correlation is demonstrated graphically in Figure 16. The old field herbs persist, then, because the absence of litter enables their light seeds to reach mineral soil and when once germinated, root competition from the larger woody species is absent.

The pine, because of its wind-borne seed, is able to invade this type of herbaceous community and populate, more or less thoroughly, such areas with seedlings, the density of the stocking depending on proximity of seed trees, quality of seed year, and amount of organic litter which has accumulated under the tall herbs. Seeding-in of the pine continues until the young trees are several feet in height and a relatively thick covering of litter has accumulated over the surface of the mineral soil and until the root network characteristic of the pine stage is closed. Most of those pine individuals, which enter

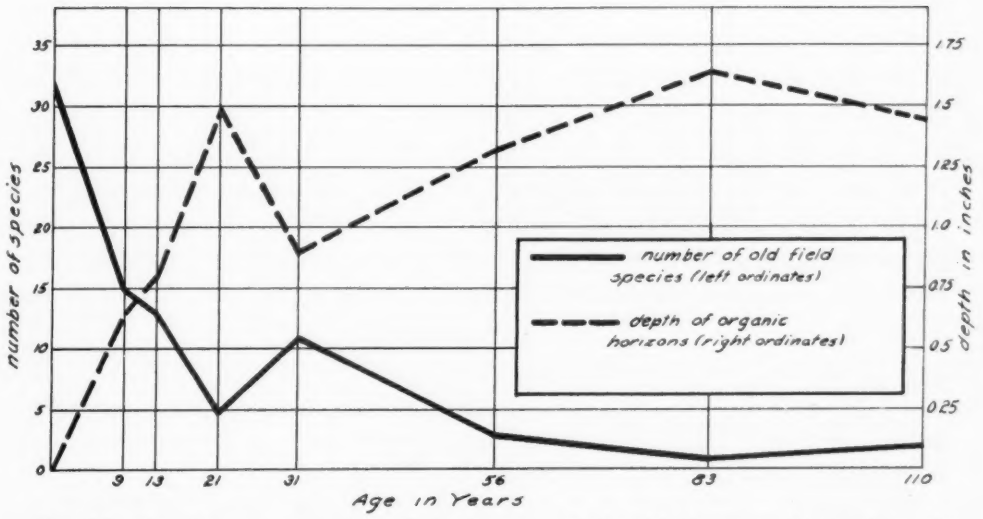

FIG. 16. Graphic representation of the inverse relationship between the total number of old-field herbaceous species and the depth of the organic horizons throughout the shortleaf pine succession.

in a dense stand after the oldest pines are taller than a few feet, never survive. From this it is evident that an even-aged stand is only approximately even-aged and occasionally individuals may vary as much as 10 years in age. From this point on, the discussion will refer only to even-aged stands which are fully stocked.

With the closing of the root network in the upper 6 inches of soil and the increase in size of trees, there is intensified competition for water, nutrients, and space. The result is a rapid decline in number of dominants as the weaker and more poorly equipped individuals die off. At the same time, the accumulated needle litter under the pines, coupled with the intense competition from the pine roots, tends to make the environment unsuitable for the old field herbs and these species are gradually eliminated. As pointed out previously, because of increasing depth of the pine litter, the light seeds of these herbs cannot reach mineral soil and so cannot germinate and become established. The high inverse correlation of —0.973 obtained between depth of litter and the presence of old field species seems to indicate one reason, at least, for the absence of such species in dense pine stands. The present results agree with those of Reed (1934) who found seeds of a great many old-field species of herbs in the organic horizons of the forest floor under shortleaf and loblolly pines. Only a few of these same species were represented in the herbaceous flora of the stands in which he worked. Kawada (1931) has shown somewhat the same thing in Japan, in that removal of litter from the forest floor under *Pinus thunbergii* results in a more xeric herbaceous flora.

The total depth of the organic remains increases rapidly at first and then more gradually as a stand approaches maturity. After a few years of occupation by pine, the decaying litter forms a zone of fermentation but it is not

until the stand is from 25 to 30 years old that the humus layer of broken-down organic matter appears. These last two layers tend to increase through succession while the layer of undecomposed litter remains practically uniform in thickness as the stand increases in age.

This accumulation of decaying and undecayed litter which adds organic matter to the soil is important in several ways. The data on thickness of these organic remains when correlated with those on water-holding capacity of the surface soil yield a highly significant correlation coefficient of 0.930. This correlation, which is graphically portrayed in Figure 17, is almost entirely

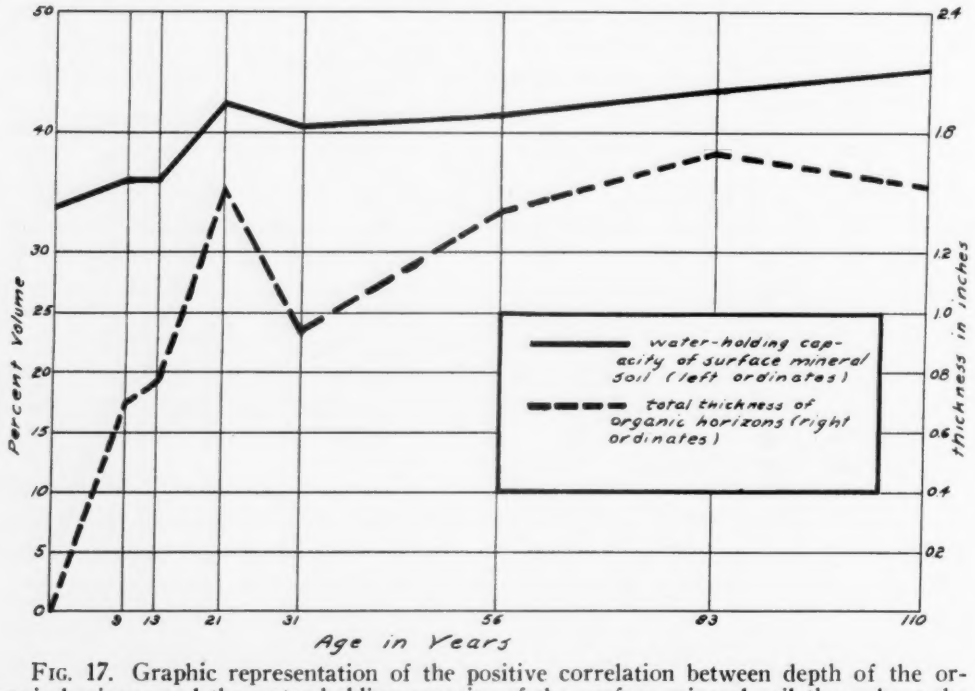

FIG. 17. Graphic representation of the positive correlation between depth of the organic horizons and the water-holding capacity of the surface mineral soil throughout the shortleaf pine succession.

dependent on amount of organic matter incorporated in the mineral horizons by leaching from above since, by reason of a coefficient of 0.884, water-holding capacity of the surface soil is shown to be highly correlated with its content of organic matter. Besides this effect on water-holding capacity through the addition of organic matter, the thickness of organic horizons also has a striking effect on reproduction of the key species of the pine-oak succession. Korstian (1927) has shown that because loss of moisture from acorns results in a great decrease in viability, a thick protective layer of litter is needed to preserve moisture necessary for germination. In the case of the present study, the first oak seedlings appear only after the pine litter has reached a depth of at least an inch. This depth is reached about the time that the stand is 20 years old. That the abundance of oak reproduction is largely governed all through the pine succession by depth of the organic remains, is

shown by the correlation coefficient of 0.639 obtained for these two factors with the present data. Although this coefficient is not statistically significant, it is large enough to suggest a positive effect of the organic horizons on reproduction of the several species of oak.

Aside from the protective influence of litter, the invasion of oaks is controlled by other factors. Water-holding capacity of the surface soil is one of these controlling factors. A simple correlation between this soil factor and density of oak reproduction shows a coefficient of 0.854 which statistically is highly significant according to Fisher's (1930) tables for the significance of values of *r*. Organic matter content in the surface soil is also highly correlated with the numbers of young oaks having a coefficient value of 0.805. Organic matter probably influences reproduction mainly in its effect on water-holding capacity and volume-weight of soil. The high correlation between organic matter and water-holding capacity has been previously pointed out and the coefficient of —0.911 shows a highly significant inverse correlation between organic content and volume-weight of the same soil. The effect of volume-weight itself on oak reproduction is readily brought out by the high inverse correlation coefficient of —0.879 between the two factors. Oak reproduction, then, seems also to increase as the soil becomes more porous and the soil of old fields and younger stands is too compact for easy penetration of oak radicles. This substantiates the results of Korstian (1927) who found that a compact soil was detrimental to the establishment of oak seedlings.

The combined effect of five of the most important edaphic factors on density of oak reproduction is shown when these six variables are subjected to multiple correlation. These five variables: thickness of organic horizons, water-holding capacity of surface soil, volume-weight of surface soil, organic matter of surface soil, and moisture equivalent of surface soil when correlated with the density of oak reproduction give a multiple correlation coefficient of 0.922. While this value is high, it is not a perfect correlation and there are other factors which might be considered as influencing the entrance and continued reproduction of oak. Since acorns are not wind disseminated and the areas under discussion are level, they can only reach the middle of a dense pine stand by being put there by animals. Squirrels probably eat most of the acorns which they bury in the litter but there are always some which escape this fate, and being naturally planted under this protective covering of litter, germinate and become established. Oaks, then, enter because the complex of factors which governs their germination and survival has been developed to a suitable point by a 20- to 30-year occupancy of old field sites by the pine community. In other words, they appear when the combined effects of root channels, fauna, and organic matter have made the soil moist and porous enough for their germination and continued survival. That this survival is also partially controlled by the morphology of oak seedlings will be pointed out later.

With this same increase in amount of litter, there is a sharp decrease in amount of pine reproduction. After a stand becomes approximately 30 years old, reproduction of pine is extremely rare. The result of this lack of reproduction, along with a decrease in the herbaceous flora before the oaks and other hardwoods are very numerous, is to give pine stands between the ages of 20 and 50 years a strikingly barren appearance as regards subordinant vegetation. Figure 3 brings out this barrenness of the forest floor quite clearly. There are probably several reasons for the failure of pine to reproduce under its own cover. A multiple correlation between density of pine reproduction and the same five edaphic factors which largely control oak reproduction yields a coefficient of only 0.601. Obviously there must be several other factors which partially control this disappearance of pine reproduction. In the first place, germination itself is probably considerably retarded by several environmental and morphological factors. Pine seed is very light and it is, therefore, unusual for it to penetrate through the increasingly deep litter and thus reach mineral soil. Barr (1930), working in British Columbia, found that spruce seeds failed to germinate when not reaching mineral soil because of inability of the seeds to absorb enough water from the highly hygroscopic humus. In shortleaf pine stands, failure of pine seed to germinate is probably the result of a combination of this lack of absorption of water with the possible detrimental effect of decreased light intensity.

If germination does take place, the seedlings seldom survive more than a year or two. On examining 1-year old seedlings of pine taken from the 31-year stand, it was found that the usual root system is extremely small, being only 1 or 2 inches long with one or two very short and weak laterals. Not much additional development occurs in the second year. This very poorly developed root system therefore penetrates to a depth of about 3 inches in 2 years' time. As has been shown, the root network closes early in the life of the stand and is almost entirely confined to the upper 6 inches of soil. It is evident from this that the poorly developed root of the pine seedling is in the zone of most intense competition. Craib (1929) has shown that during dry periods, trenched areas, in which the tree root competition is eliminated, have two to nine times as much available water in the first 6 inches of mineral soil as comparable untrenched areas. Toumey and Kienholz (1931) have conclusively demonstrated that this increased amount of available water during times of stress in the trenched areas, results in a very luxuriant herbaceous and low woody vegetation as compared to the barrenness of the usual forest floor with normal root competition. Similar studies reported by Korstian (1934) in the Duke Forest have shown comparable results. During dry periods there is undoubtedly no available water in the first 6 inches of soil due to its extraction by roots of dominant trees. This obviously results in the death of the seedling pine, since its weak, shallow root system occurs in the zone of most severe root competition.

While young pine reproduction fails to survive dry periods, the presence of numerous young oaks and other broad-leaved trees indicates the ability of these species to survive even though the surface soil is devoid of available moisture. The edaphic factors which condition the entrance and continued reproduction of oaks have been previously pointed out. However, why should oaks and certain other woody genera be able to survive through critical periods of soil moisture, while pine cannot, in spite of the obvious betterment of soil conditions? Morphological investigations on the seedlings of oak, hickory, tulip poplar, and red cedar in the 31-year stand reveal that these species all have uniformly strongly developed deep root systems when young. These observations agree with Toumey's (1926) findings that oak and hickory seedlings develop a 10- to 15-inch taproot the first year and that the red cedar and tulip poplar seedlings produce a deep, much-branched root system during the first year. In Figure 18, the root systems of one- and two-year old shortleaf pine seedlings are contrasted with those of a one-year old white oak and a three-year old black oak. Striking differences in depth of the root systems and also in thickness of the taproots are very apparent. The extensive root systems of tulip poplars two years old are illustrated in Figure 19. This figure shows the much-branched character of the root system of the seedling tulip poplar which aids greatly in the survival of this species under pine after once becoming established. The well-developed root system of a two-year old red cedar is shown in Figure 21.

Because these deeply penetrating root systems pass through and beyond the zone of greatest pine root competition, they survive the first season and considerably strengthen their position during the second year. This does not imply that they are entirely unaffected by the pine competition but they are, by virtue of their deeper root systems, better able to withstand periods of stress. Another characteristic in favor of the survival of these species is the ability to produce sprouts or new shoots from the base of the stem when the aerial parts are killed back by desiccation. This is especially true of oaks and tulip poplar. In Figure 19, the aerial parts of tulip poplar seedlings are two years old. However, the one with the largest root system exhibits the common characteristic of seedlings of this species to sprout and a new shoot has originated from the base of the dead stem.

Examination of the seedlings of red maple and dogwood, typical secondary trees, shows a highly developed, much-branched root system which would favor survival. The only shrubs examined were young individuals of *Viburnum rafinesquianum*, practically the only shrub present in the closed young pine stands. The root systems of this species are not only deep but also extremely thick and fibrous. The extensive fibrous root systems of young individuals of both Viburnum and Cornus appear in Figure 20.

Since these findings point to the fact that seedlings of woody species surviving pine competition must have either deeply penetrating taproots or a

highly developed fibrous root system during the first few seasons of growth, the question of herbaceous root systems arises. Since the herbs are rather rare in such dense pine stands, it is evident that most of them are not fitted

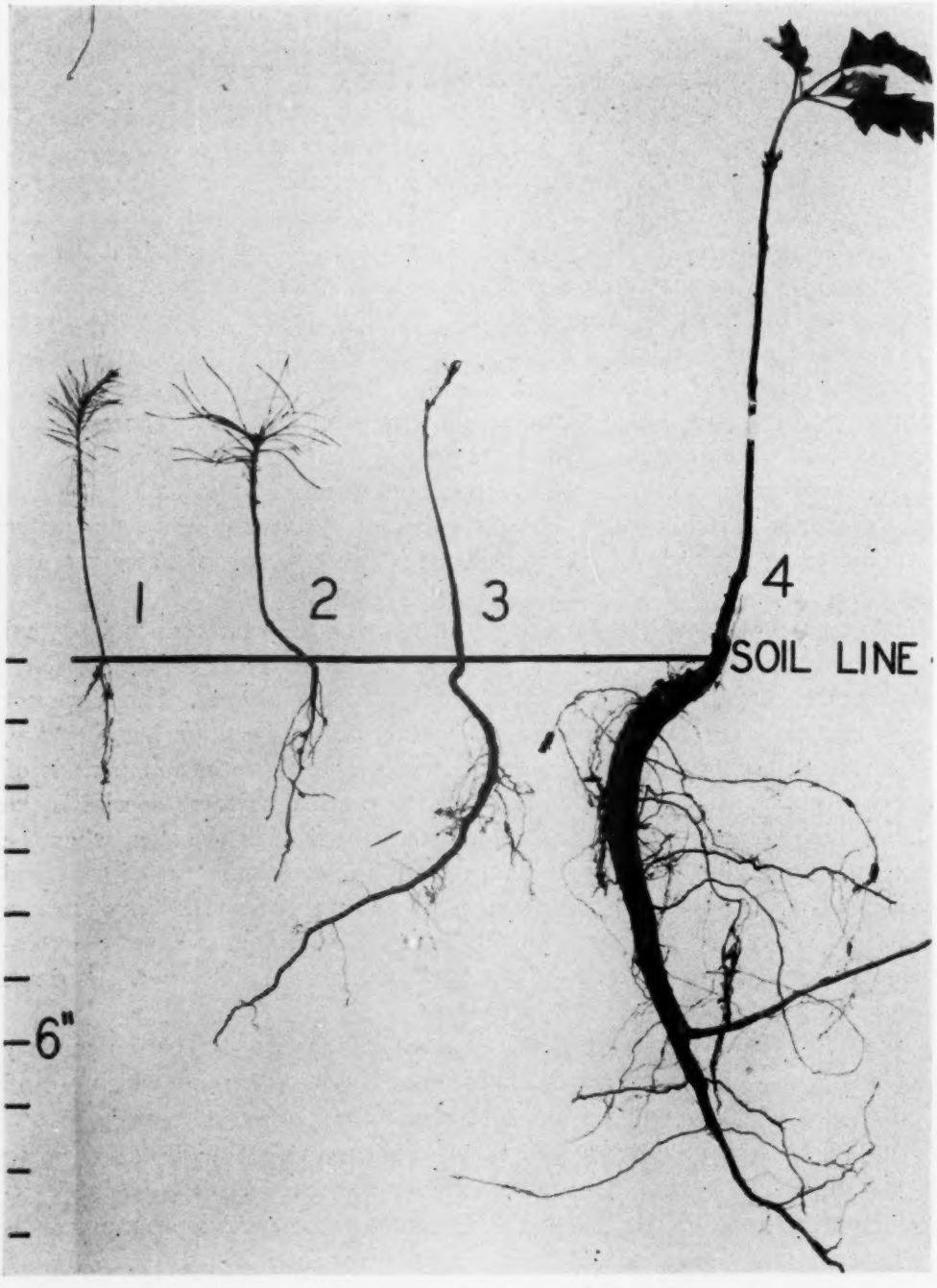

FIG. 18. Root systems of one-(1) and two-(2) year old shortleaf pine seedlings contrasted with the root systems of a one-year old white oak (3) and a three-year old black oak (4). All are from the 31-year old stand.

for survival even though germination takes place. The outstanding feature of the herbaceous flora is that it is made up almost entirely of perennial xerophytes. This bears out the assumption that the surface soil is extremely

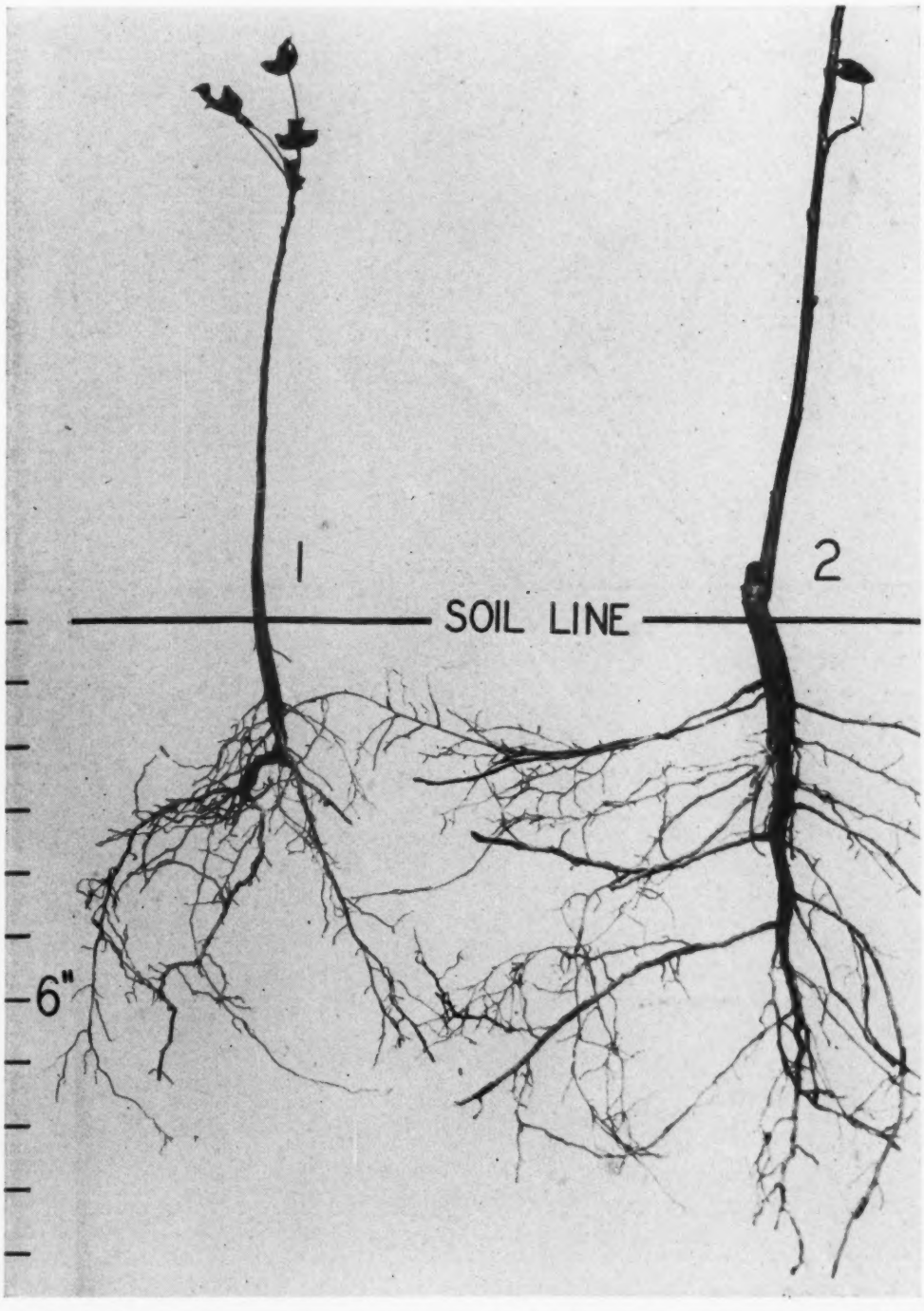

FIG. 19. Extensive root systems of two-year old tulip poplars. The one on the right has been killed back once and has sprouted from a dormant bud at the base of the stem. Both are from the 31-year stand.

dry at times as a result of root competition. The soil under a closed dense pine stand during the driest part of the year might well be compared to that of an exposed rocky ridge. It is powdery and probably entirely lacking in

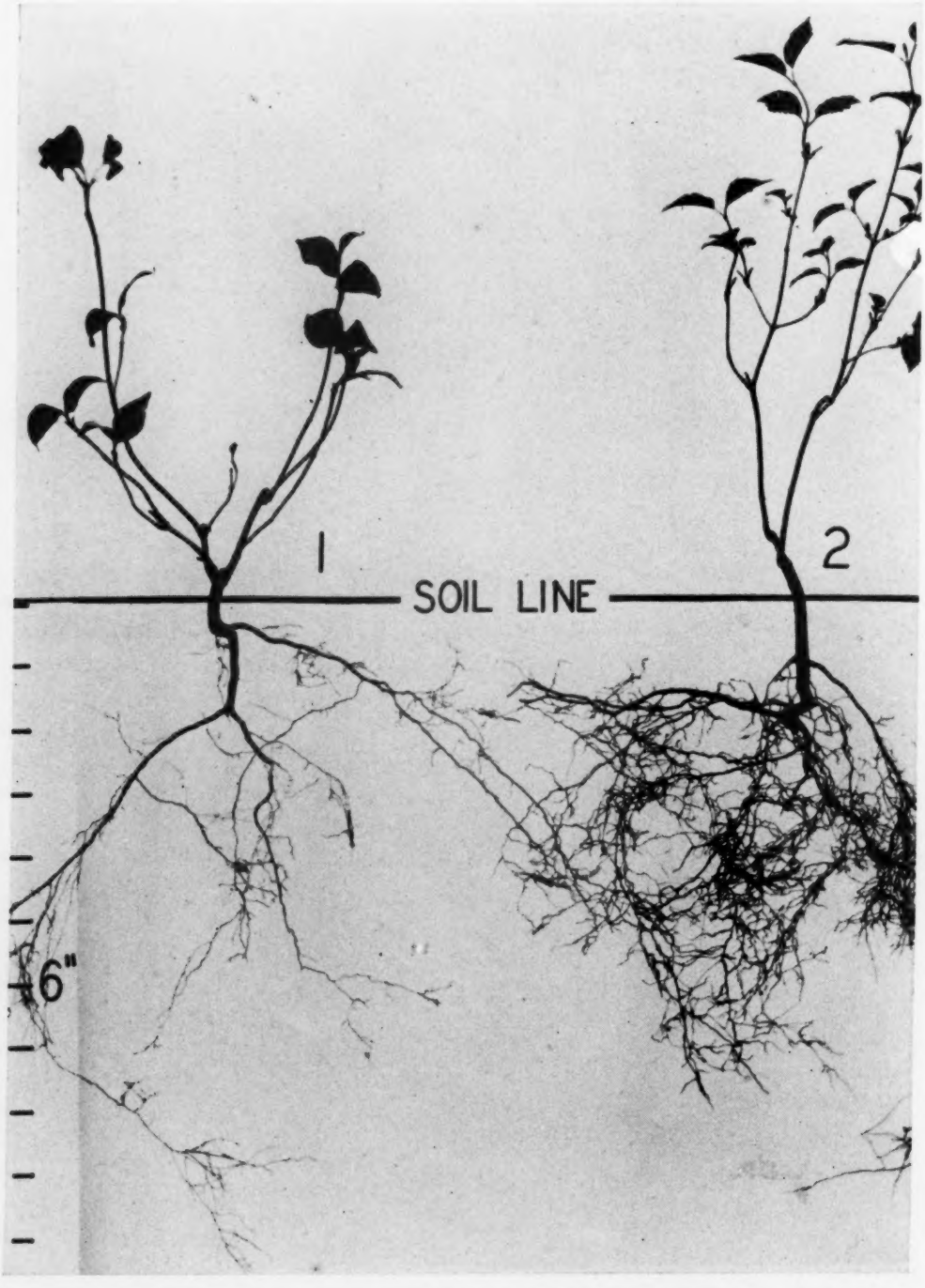

FIG. 20. Extensive fibrous root systems of flowering dogwood, *Cornus florida* (1), and downy viburnum, *Viburnum rafinesquianum* (2). Both are three years old and are from the 31-year stand.

available water. Some species, such as *Chimaphila maculata*, the most common herb in these stands, are heavily cutinized and evergreen. Others, such as *Elephantopus tomentosus* and *Gnaphalium obtusifolium* have the leaves covered with hairs. These characteristics result in decreased loss of water by transpiration and so physiologically fit the species for survival in such precarious habitats. The root systems of these plants are also fairly deep. The relation between depth of litter cover and number of old-field herbaceous species has been previously pointed out. Characteristically, the old-field species which survive and the typical pine forest herbs are perennials and reproduce vegetatively by means of stolons and underground stems. Because of these characteristics, many species can persist and spread in spite of the failure of their seeds to reach mineral soil. This is exemplified by *Chimaphila maculata, Gnaphalium obtusifolium,* and several species of Solidago. A mature plant of Chimaphila with underground shoots and deep roots appears in Figure 21.

About the same time as the first appearance of oak seedlings, the A_1 horizon begins to develop. It overlies the brownish "plowed" horizon and gradually replaces it. Because of its high content of organic matter which constantly increases, it has an increasingly high water-holding capacity, an active soil fauna, and a good crumb structure. The great hygroscopicity of humus is apparent from increased moisture equivalent of the surface soil as organic matter is added. The highly significant correlation coefficient of 0.949 between organic matter and moisture equivalent in this horizon bears out the dependence of a change in moisture equivalent on organic matter in the soil. This horizon gradually grows in thickness and from the addition of organic matter, the death of roots, and the activities of small animals becomes light and porous. This is an indication that the soil is beginning to return to its virgin forest condition.

As a pine stand approaches its middle age, the broad-leaved trees which have successfully become established, form a definite secondary arborescent stratum. Figure 9, an external view of an 85-year stand, shows this stratum of hardwood trees under the canopy of pine. The outstanding tree in this stratum is flowering dogwood which is always a secondary tree, rarely becoming dominant. Other trees, such as oaks, hickories, red maple, and tulip poplar, make up part of this understory. Almost all the species in this stratum also have abundant reproduction. The overstory pines die off gradually and with the death of each one, the understory hardwoods gain a distinct advantage. In the mature pine stand, the dominants are giving way to hardwoods as is shown by comparisons of frequency and density of the two groups. Figure 4, taken inside this stand, shows a few scattered old pines surrounded by a dense undergrowth of these hardwood trees. The surface root network of pine is still present but the increased abundance of deeper roots testify to the fact that oaks, hickories, and other deeply rooted species are firmly estab-

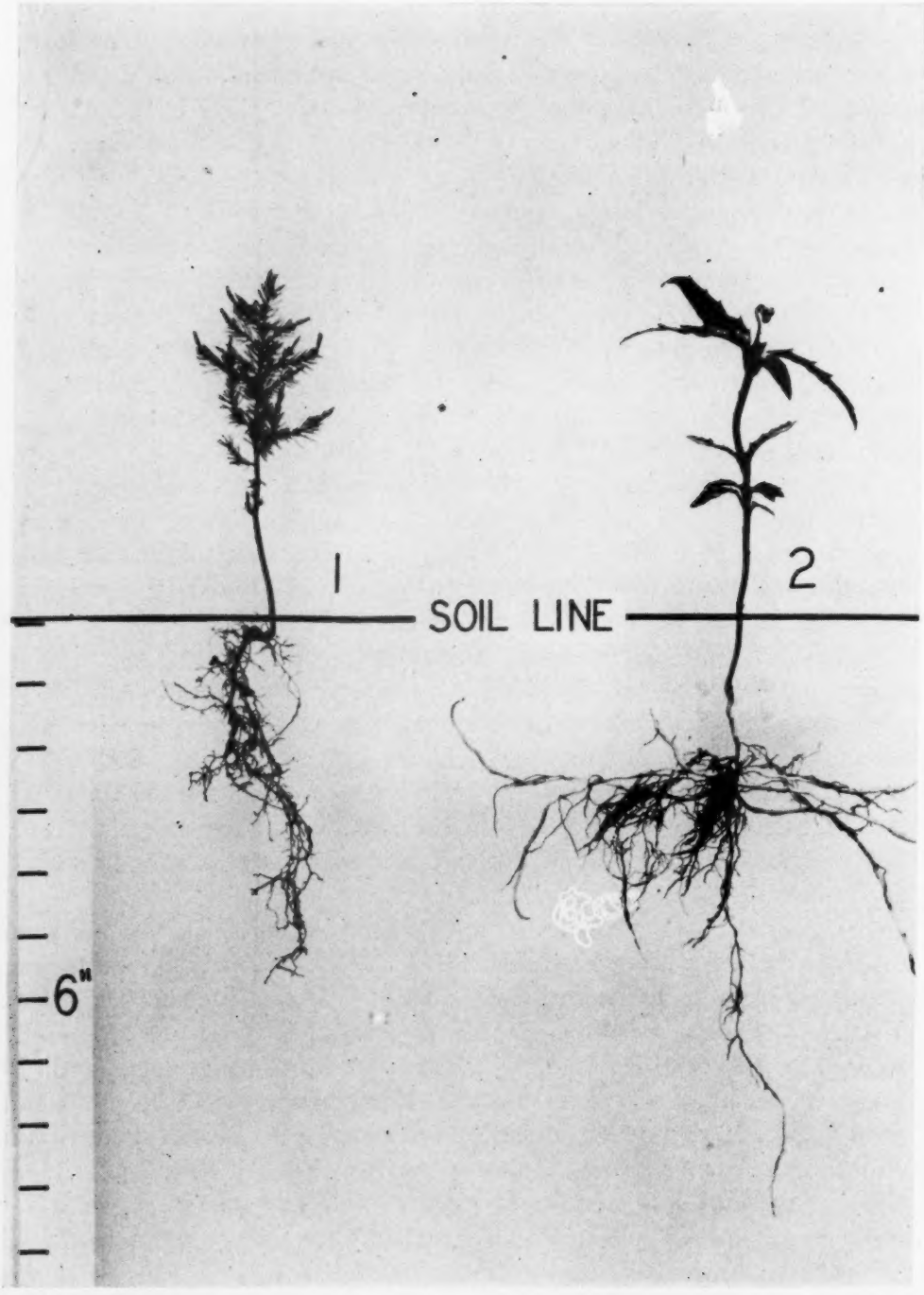

FIG. 21. Characteristic root systems of a two-year old red cedar (1) and a mature plant of *Chimaphila maculata* (2). Note the extensive rhizomes of the latter. Both specimens are from the 31-year old stand.

lished and .at the soii will be utilized by roots to a much greater extent than in the pine stage.

Oaks and hickories are still only secondary trees in the mature pine stand but with the death of each mature pine, the nearest hardwoods are released from suppression nd they rapidly assume dominance. Certain species, flowering dogwood, for instance, continue reproducing abundantly but never become more than secondary trees. It seems probable that these species make up a type of understory community which is dependent on an overstory but independent of the floristic composition of that overstory. If this is true, the dogwood synusia should continue on over into the hardwood community or phytocoenosis following pine. Observations on such hardwood stands reveal that this is the case and that this understory community is as well-developed there as it is in the pine phytocoenosis.

All through the pine succession, an herbaceous flora typical of hardwood stands has gradually been developing and by the time the pine is mature, this flora is fairly distinct and, with additions, continues over into the deciduous stand.

Pine, then, is a preliminary and temporary stage in the return to the climax forest. It is able to invade but, because of its own effect on the soil factors, especially those affecting soil moisture, is unable to maintain itself. However, by adding organic matter and by the formation of root channels, it prepares the soil for other species which successfully invade and eventually replace it by being better adapted to competition in the seedling stage and by utilizing the soil to a greater extent. Pine, through its effect on the soil, initiates the swing of the pendulum back toward a climax forest soil and the incoming hardwoods will continue this effect until sometime in the future the forest will again reach that near-stable organismo-environmental complex, the climax community.

SUMMARY

A quantitative analysis of the vegetation and certain soil factors was made on a successional series of shortleaf pine stands in the Duke Forest near Durham, North Carolina. These stands are on very nearly identical areas as regards climate, topography, and soils. The stands studied were limited to nearly level areas of a light-textured Lower Piedmont soil of good site quality. The vegetation was analyzed by means of several sizes of quadrats; a particular size being selected as best suited to the vegetation in any one vegetational stratum. Trenches were dug in each stand for the collection of soil samples for analysis. Soil studies included mechanical analysis, determination of amount of organic matter, moisture equivalent, water-holding capacity, volume-weight, air capacity, and profile development. The roots were mapped on vertical profiles by size classes. Studies were made of seedling root development of the more important species in the succession. The

results were correlated and integrated by the statistical method of calculating simple and multiple correlation coefficients between the several vegetational and soil factors. The important results are summarized as follows:

Vegetation.

1. Abandoned agricultural land on light-textured Piedmont soils is first occupied by a relatively shallow-rooted herbaceous community dominated by broom-sedge *(Andropogon virginicus).*

2. Shortleaf pine invades these fields, often in great numbers, due to its wind-borne seeds.

3. Shortleaf pine is able to germinate and survive because of exposed mineral soil and low root competition.

4. Density of the dominant pines is very high when the stand is very young, in some cases averaging nearly 3,000 stems per acre. This density falls rapidly at first and then gradually levels off as the pines reach maturity and then lose their dominance. In the oldest stand studied, 110 years of age, there are only 60 pine stems per acre.

5. The closing of the network of pine roots, which through this stage of succession is mainly in the first 6 inches of soil (56 to 64 percent of the total roots as compared to 17 to 25 percent in the second 6 inches), occurs very early in the life of a stand. This, combined with the increasing depth of litter accumulating under pine, causes the disappearance of the old-field herbaceous species. A highly significant inverse correlation coefficient of —0.973 was obtained between depth of pine litter and presence of old-field herbs during succession.

6. The first oak seedlings appear at the time the stand is about 20 years old, when enough litter has accumulated to protect the acorns against loss of viability through desiccation and the surface soil has become porous and sufficiently retentive of moisture for their survival. The five most important variables affecting the entrance of oaks are: thickness of organic horizons and water-holding capacity, volume-weight, organic matter, and moisture equivalent of surface soil. These five factors, when correlated with the density of oak reproduction show a high multiple correlation coefficient of 0.922. The principal invading oaks are *Quercus rubra, Q. velutina,* and *Q. alba.*

7. Hickory reproduction does not enter until a few years after the first oaks appear. The principal hickories are *Hicoria alba* and *H. glabra.*

8. Pine reproduction declines rapidly in the younger stands and finally disappears altogether after the stand reaches middle age.

9. The barren appearance of the forest floor in the middle-aged stands is probably due to severe root competition from the dominant pines.

10. Pine seeds germinate only where they can reach mineral soil.

11. Once germinated, seedling pines under dominant pines seldom survive more than one or two years because of the very short, weak root system lying in the zone of intense competition from the dominant pines.

12. Surviving hardwood seedlings, such as those of oaks, hickories, and tulip poplar, persist because they develop either a long taproot or a much-branched fibrous root system during the first year. Many of these same species also sprout when killed back.

13. Most shrubs and herbs of the middle-aged pine stands also have well-developed root systems. The herbs are mostly perennial and usually reproduce vegetatively by stolons or rhizomes as exemplified by *Chimaphila maculata.*

14. A well-defined understory becomes evident by the time the stand reaches middle age. This layer is characterized by flowering dogwood and red maple and is present in the oldest pine stands and also in hardwood stands following pine.

15. An herbaceous flora characteristic of hardwood stands gradually develops as the pines grow older. This flora is typified by *Polygonatum biflorum, Peramium pubescens, Aristolochia serpentaria, Hexastylis virginica,* and *Viola* spp.

16. In mature stands, pine is beginning to lose out as is shown by its decreasing density and frequency. Each over-mature pine which dies is replaced by deeper-rooted hardwoods which its death releases from suppression.

Soils.

1. The surface soil in the herbaceous old-field community has a relatively high volume-weight (1.346), a low water-holding capacity (33.705 percent), a low organic matter content (less than 1 percent), and a low moisture equivalent (6.84 percent).

2. The profile of the soil occupied by this old-field community is characterized by a thick, brown "plowed" horizon at the top averaging about 12 inches in thickness.

3. The brown "plowed" zone grows thinner in an upward direction and is replaced by a blackish gray A_1 horizon which develops over it. This replacement occurs between ages of 20 and 30 years.

4. With the appearance of the A_1 horizon, there comes a decrease in volume-weight and an increase in water-holding capacity of the surface soil. The first is due to a combination of root channels, organic matter, and animals. The second is due mostly to the effect of increased organic matter and to some extent to greater porosity of the soil.

5. A progressive decrease in volume-weight and increase in water-holding capacity of the surface soil continues through the pine succession. The former averages only 1.029 in the mature stand, while the latter averages over 45 percent.

6. Through the addition of organic matter, there is also an increase in the moisture equivalent of the surface soil. A highly significant correlation

coefficient of 0.949 between these two variables shows the close dependence of any change in moisture equivalent upon a change in organic matter content.

7. No pronounced trend is exhibited by the air capacity of the soil during the pine succession, at least in the stands studied.

8. There seems to be no significant change in relative amounts of inorganic soil-fraction sizes during the pine succession.

9. The profile seems to be affected by pine only in the first 6 inches of soil. An A_1 horizon has developed in this region. This horizon becomes lighter and more retentive of water throughout the pine succession because of the addition of organic matter, the formation of root channels, and the activities of the soil fauna. These causal factors in soil change are conditioned by the presence of pine vegetation which in turn is changed and eventually disappears because of its effect on its own environment.

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